IUBS Unesco MAB SCOPE

A NEW LOOK AT ECOTONES

Emerging International Projects on Landscape Boundaries

Edited by

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In Collaboration with
the US. MAB National Committee

Biology International

SPECIAL ISSUE 17

A NEW LOOK AT ECOTONES:

EMERGING INTERNATIONAL PROJECTS ON LANDSCAPE BOUNDARIES

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Special Issue - 17
Biology International

The International Union of Biological Sciences
News Magazine

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ACKNOWLEDGEMENTS

The Editors wish to thank SCOPE, MAB, IUBS and IIASA which have been instrumental for the organization of the technical workshops on ecotones and for the publication of this special issue. In this respect, gratitude is extended to Dr. Talal YOUNES, Executive Secretary of IUBS, who has made possible this publication. Support for this project came from the Centre National de la Recherche Scientifique (CNRS), France ; the Department of Forest Science, Oregon State University, USA ; and the Ecological Society of America. The Editors thank the authors of the different articles for their cooperation, and Dr. Mel DYER, UNESCO, for stimulating discussions on ecotones. Finally, they offer thanks to Ms. Nadine COMBES, who has typed all the manuscripts and has prepared this issue in camera-ready form, Ms. Annie DAO and Maryse GAUTIER for proofreading, and the graphic artists Denis LACOMBE, Claude LACOMBE and Joseph VILANOVA who prepared the illustrations. All these collaborators from CNRS, with their talent and diligence, have helped making sense of manuscripts of differing languages and styles.

PREFACE

All ecosystems of the world are affected by unprecedented human disturbance, in regard to both the intensity and variety of impacts. The consequence of such disturbance and of the complexity of associated interactions is an increased globalization of environmental problems and a decrease of their predictability. This globalization implies an enlargement in the spatial scale of the different disturbances and a strong "contraction" of the temporal scale, so that ecological processes occur over a larger space and in a shorter time.

Humans have become the main agent of change and the main selective force in evolutionary terms. It is not the first time in the history of mankind that the spatial scale of impacts has abruptly increased, and the scale of time has rapidly decreased. This was the case, for instance, at the time of the great discoveries (about 1500 A.D.), or during the industrial revolution, when similar impacts were simultaneously acting on the diverse ecosystems of the biogeographical realms of the world.

Never in the past, however, has the ecological globalization been so pervasive as at present. The principal global driving forces are of an economic nature: the interdependence of economies (world market price systems) all over the world. This interdependence, unfortunately, does not derive from an established cooperation between and among countries in different parts of the world, but rather because of conflicting economic interests within and between countries.

The newly emerging economic conflicts, resulting from different geopolitical configurations, or from the strong disorder in the currencies exchange (e.g., the U.S. dollar fluctuations), make it more and more difficult to predict possible trends of ecological impacts. Pressure on given resources can shift suddenly from one region to another according to global market incentives and requirements, the relative weakness of the local currency, and changing labor costs. Many "surprise" effects have occurred during the last decade, and many more are likely to happen in the near future (see Svedin and Aniansson 1987)[1].

Such globalization of driving forces and interconnectivity of economies does not mean that ecological impacts and responses are the same everywhere. It only means that local phenomena are increasingly determined by complex global interactions and not necessarily by locally-based decisions. For instance, countries of the European Community may be inclined to decrease their pressure and interest on agricultural lands, because of their already enormous food excedents (and the high cost of production and storage). Conversely, many developing countries may be obliged, at the same time, to further impact their fragile ecosystems and increase their production at the limit of ecological irreversibility in an attempt to overcome their huge and evergrowing international debts (and to try to ensure the basic needs of food and alimentation to their populations).

Therefore, as a consequence of this interlinked web of conflicting economic interests at different levels, one can see in some countries a progressive regeneration of natural vegetation, because of a partial abandonment of agricultural lands. Conversely, in other countries large forested areas are being fragmented to facilitate agricultural colonization, or already-cleared areas are being further exploited up to their desertification. Furthermore, the size of agricultural units tends to become larger, through the elimination of hedges, fences and "bocage", in order to facilitate the agricultural mechanization and to lower use of manpower and production costs.

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[1] Svedin, V. and B. Aniansson, editors. 1987. Surprising futures. Swedish Council for Planning and Coordination of Research, Stockholm, Sweden. 128 p.

Landscapes of the world are therefore changing as regards their expansion, contraction, and fragmentation. Managing these newly and rapidly changing environments implies an understanding of the most sensitive parts of landscape interactions: the boundaries that are being shaped and reshaped mostly by human action.

In addition to this widening crisis of globalization due to a large-scale interdependence between global economy and the world environment, there is another impending global crisis: global climate change. The intricate confrontation of varied human impacts, at different scales of space and time, is leading to a phenomenon which is unique in the history of mankind, that of the man-induced biospheric change of climate (Malone and Roederer 1985)[2]. This change is expected to produce a warming of the planet in a few decades. The increase of temperature is likely to be uneven from one to another ecological zone, and be concomitant with diverse changes in run-off and evapotranspiration. The increased frequency of extreme events that will co-occur with early climatic change, and is likely to have greater impact on ecological and socio-economic factors (Wigley 1985)[3], will further increase the complexity and unpredictability of this process of change.

Undoubtedly, these successive waves of globalization will produce repeated modifications of the shape of landscapes. Acting on populations and ecosystems already under stress because of human action, these waves will increase the risk of species extinction, and restructure the configurations of the boundaries between ecosystems. These events concern not only terrestrial ecosystems, but also -because of changing run-off and raising of sea level- the interactions between terrestrial and riverine or coastal ecosystems.

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[2] Malone, T. F. and J. G. Roedere, editors. 1985. Global Change. ICSU Press and Cambridge University Press, Cambridge, UK, 512 p.

[3] Wigley, T. M. L. 1985. Impact of extreme events. Nature, 316: 106-107.

"Interaction is the intrinsic" (see di Castri 1976)[4], and most interactions between the various components of the landscape will occur in the boundaries, usually called "ecotones". Within this context of successive global crises, the notion of ecotone is likely to become a core concept -as regards both theory and practice- for early monitoring, understanding and managing this change.

As defined by the members of a working group which met in Paris in early January 1987, and was chaired by the senior editor of this special issue of Biology International, the ecotone is a:

> *"Zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales, and by the strength of the interactions between adjacent ecological systems."*
> (see Holland, this issue)

This definition fits well within the context of human-made alterations of spatial and temporal scales, as illustrated by the statements above. It also puts a proper emphasis on interactions for measuring the connectivity of the system. Such a system can be envisaged at any hierarchical level from populations to the biosphere, at any space from a few centimeters to thousands of kilometers, according to the scale of a given disturbance, but also following the perspective of the research worker, the working hypothesis and the problem to be tackled.

Accordingly, the concept of ecotone, as applied in the different articles of this special issue, is well in agreement with the present multi-scale

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[4] di Castri, F. 1976. International, interdisciplinary research in ecology: Some problems of organization and execution. The case of the Man and the Biosphere (MAB) Programme. Human Ecology 4: 235-246.

approach of ecology (di Castri 1987)[5], which overcomes the traditional split-down between population, community and ecosystem ecology, between reductionism and holism, etc.

Again within the present context, one of the main shortcomings for tackling environmental problems, especially those occurring at a very rapid pace of change, is the institutional disorder. Institutions dealing with the environment, both at the national and international levels (di Castri 1985)[6], are too often involved in sterile competition and fights of interest. This undermines the overall conceptual and operational understanding of the environment as a whole.

In the developments leading to the launching of these projects on ecotones, it has been tried, as much as possible, not to be "contaminated" by the "institutional-fight syndrome" and to involve, from the very beginning and with a shared responsibility, the main organizations concerned. This was also done in order to decrease overlap and increase interaction between institutions.

The two main institutions involved in the preparation of this issue have been SCOPE (Scientific Committee on Problems of the Environment), belonging to the ICSU family, and the Man and the Biosphere (MAB) Programme of Unesco. Both SCOPE and MAB emerged in the late 1960s and early 1970s,

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[5] di Castri, F. 1987. Towards a common language from molecular biology to biospheric ecology? Biology International, Special Issue 15: 3-9.

[6] di Castri, F. 1985. Twenty years of international programmes on ecosystems and the biosphere. An overview of achievements, shortcomings and possible new perspectives. Pages 314-331 in T. F. Malone and J. G. Roederer, editors. Global Change. ICSU Press and Cambridge University Press, Cambridge, UK: 314-331.

before the holding of the United Nations Stockholm Conference on the Human Environment in June 1972. SCOPE and MAB evolved from an early phase of latent competition, through a rather long phase of mutual ignorance (with some rewarding examples of active cooperation), towards the present phase, when the possibility of being complementary in many issues appears more and more evident.

As a matter of fact, SCOPE and MAB do not share the same "ecological niche". The MAB Programme is part of Unesco's activities. It is therefore an intergovernmental programme; its "projects" are operational research activities in the field, and attempt to have a managerial objective. On the other hand, SCOPE is non-governmental in nature; its "projects" have as a main objective the preparation of state-of-knowledge syntheses on critical environmental issues.

It is true that separation cannot be so sharp. A research project in the field should have a phase of preliminary synthesis of the existing knowledge. Conversely, a synthesis report which underlines gaps of knowledge, can almost spontaneously be an incentive for the launching of research to fill these gaps. Therefore, there is ample room for complementarity between MAB and SCOPE projects. Some thematic overlap is even desirable in this respect.

In addition, both SCOPE and MAB may provide useful inputs and background information for the newly launched International Geosphere-Biosphere (IGBP) "Global Change" Programme (ICSU 1986)[7]. Landscape boundaries can be considered as early indicators of climatic change. It is evident that SCOPE and MAB do not have the servicing of IGBP as their principal aim. Rather,

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[7] ICSU. 1986. The International Geosphere-Biosphere Programme. A study of global change. International Council of Scientific Unions, Paris, France.

by pursuing their traditional role, they can be important pillars in the construction of the so complex machinery of IGBP. Furthermore, -and this is particularly true for SCOPE given its very light and flexible organizational structure- the investments strictly focus on scientific outputs. The main concern is on quality control, and this can favor the "scientific more than institutional" and "bottom-up" approach advocated by di Castri (1985)[6] and Schneider (1987)[8] for implementing international programmes like IGBP.

The involvement of the International Union of Biological Sciences (IUBS) should also be mentioned, as a good example of inter-institutional cooperation. The Secretariat of IUBS participated in all these activities and made important conceptual contributions. This close cooperation has been crystallized in a tangible way through the publication of this special issue of the IUBS Journal, Biology International.

After an introduction, where an attempt is made to give some theoretical backing to the concept of ecotone, the results of the joint technical consultation of SCOPE and MAB, held in Paris, France, in January 1987, are presented, and a general framework for the two emerging international projects is set-up. The next article describes the MAB project more in detail, as it was envisioned at a planning meeting of the MAB Scientific Advisory Group in Toulouse, France, with special emphasis given to land-inland water boundaries. The final article underlines the main elements of the SCOPE project, as elaborated in the meeting of the SCOPE Scientific Advisory Committee (SAC) on Ecotones that met in Laxenburg, Austria, and was organized in cooperation with IIASA (International Institute of Applied Systems Analysis).

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[8] Schneider, S. H. 1987. An international program on "Global Change": can it endure? - An editorial. Climatic Change 10: 211-218.

It is hoped that the inter-institutional cooperation between SCOPE, MAB, IUBS and IIASA will be further strengthened by this joint effort. However, it has been the main interest of the editors and contributors to this issue that individual scientists, irrespective of their affiliations, be challenged to pursue research on ecotones.

20 January 1988

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ECOTONES: WHAT AND WHY ?

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Abstract. The ecotone concept is widely recognized by ecologists but theory on ecotones remains underdeveloped. Traditionally, ecotone is defined as a transition zone between plant communities. Recent research on landscape boundaries, however, suggests that a broadening of the ecotone concept is desirable. In this paper, we draw on patch dynamics theory and hierarchy theory to offer a rationale for applying the ecotone concept to ecological systems of many types and spatial/temporal scales. We then explore questions on the role of ecotones in landscapes including: (1) To what extent do ecotones influence the flow of energy, materials, and organisms across landscapes?; (2) Do unique patterns of biodiversity occur in ecotones?; and (3) How should ecotones be managed to maintain or produce desirable landscape patterns? We conclude that additional research on these topics holds promise for advancing ecological theory and improving landscape management. Studies on ecological boundaries are especially important now because humankind is having an unprecedent impact on terrestrial, aquatic, and marine systems. The challenge to managers is to harness the human ability to disturb ecological systems in order to optimize landscape characteristics.

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INTRODUCTION

The ecotone concept has a long history in ecology. Some of the initial studies in plant ecology were on the transition zones between adjacent communities (Clements 1897, Livingston 1903, Griggs 1914). Ecotone is derived from the greek roots "oikos" (household) and "tonos" (tension), and Clements (1905) described an ecotone as a tension zone where principal species from adjacent communities meet their limits. The observation that some ecotones are relatively rich in species, containing representatives from each contiguous community as well as edge specialists (Shelford 1913), become known as the "edge effect" (Leopold 1933). Over the years the ecotone concept has become entrenched in ecology, and virtually all introductory texts offer some treatment of the topic (e.g. Weaver and Clements 1928, Daubenmire 1968, Odum 1971).

Despite this wide recognition of ecotones, a rigorous theoretical examination of the concept has generally gone wanting (but see van Leeuwen 1966, Daubenmire 1968, van der Maarel 1976). Many ecologists chose to avoid the complexities of patch edges or interactions between patches and worked in the centers of relatively homogeneous systems. The International Biological Programme, for example, conducted studies within, rather than in the junction between, biomes (e.g., Le Cren and Lowe-McConnel 1980). This approach has been reasonably successful and much has been learned about how events within an ecological system influence the structure and functioning of that system.

Many ecologists, however, now recognize that ecological systems are often heterogeneous and composed of components of differing structure and dynamics (Pickett and White 1985). Collectively, the dynamics of these components or patches strongly influence the characteristics of the systems they comprise (Shugart 1984). This patch dynamics paradigm offers a strong theoretical framework for studying ecotones. Ecotones represent the transition zones between patches and as such, they can be defined and classified relative to the types and scales of patches they separate. Also, the dynamics of ecotones across space and through time can best be examined within the context of patch dynamics. Conversely, patch theory will benefit from consideration of landscape boundaries. Ecotones may strongly influence interactions between patches and ultimately affect landscape-level behavior (Wiens et al. 1985, Johnston and Naiman 1987). Moreover, ecotones may affect local and regional biotic diversity because they provide unique habitats, favorable for some species but inhospitable to others (Noss 1983).

In this paper we draw on patch dynamics theory and hierarchy theory to offer a rationale for broadening the ecotone concept for application to ecological systems of many types and spatial/temporal scales. The role of ecotones in landscapes is then considered. We review the developments indicating that interactions between landscape elements strongly influence landscape dynamics and consider the extent to which ecotones modify these interactions by controlling the flows of energy, materials, and organisms between landscape elements. Next, patterns of biodiversity in ecotones are explored. Finally, we describe the accelerating rate at which human activities are altering the boundary structure of terrestrial and aquatic systems and suggest that consideration of boundary dynamics is important in landscape management.

AN EXPANDED VIEW OF ECOTONES

Traditionally, "ecotone" has been used to denote an intersection between plant communities where there is a relatively abrupt change in vegetation structure or composition (Daubenmire 1968, Odum 1971). The term is most frequently applied to transition zones of intermediate spatial scale (10's m to 100's m) such as those between woodlots and fields (e.g. Gates and Gysel 1978, Helle and Helle 1982, Kroodsma 1982) or between sharply defined biomes (Carpenter 1935, Curtis 1959). Some ecologists now see advantages in applying the concept more widely, to transitions between ecological systems of diverse types and spatial scales (e.g., the SCOPE/MAB Working Group on Ecotones. See Holland, this issue). This interest in enlarging the concept is largely a result of recent developments in the patch dynamics paradigm.

Patch Dynamics

Ecologists have long recognized that most ecological systems are composed of several distinct components and are, thus, heterogeneous. Watt (1947), for example, observed that disturbance and internal biotic processes cause vegetation in a forest to be patchy, with tree-fall gaps containing early successional species interspersed with patches of older vegetation. This led Watt to view a landscape as a dynamic mosaic of patches of differing ages, compositions, and structures. This patch dynamics model has been widely embraced by ecologists and applied to genetic, population, and landscape level problems in both terrestrial and aquatic systems (see Pickett and White 1985).

Patches may be deliniated by a variety of criteria (Forman and Godron 1986). Most simply, they are areas with greater similarity in some attribute (e.g. gene frequency, species composition, structure, resource distribution) than the system as a whole. The term implies a relatively discrete spatial pattern, but does not establish any constraint on patch size, internal homogeneity, or discreteness (Pickett and White 1985). "Patch dynamics" emphasizes that patches are ephemeral, maintaining a specific set of characteristics for only some finite period of time. Patches may arise or disappear as a result of agents of change including discrete perturbations (e.g. fire, frost, herbivory, earthquakes) and environmental fluctuations (e.g. climate cycles) (Delcourt et al. 1983, Hansen and Walker 1985). They may also be a product of internal biotic processes such as growth or senescence (Watt 1947, Urban et al. 1987). Because such events are common in ecological systems, the spatial patterning of most landscapes is dynamic through time.

One reason why this paradigm is popular is that it is robust relative to temporal and spatial scale. It has been employed in studies of, for example, plant microsites (Whittaker and Levin 1977), badger mounds (Platt 1975), tree-fall gaps (Shugart 1984), rivers (Naiman et al. 1988a) and regional vegetation patterns (Harris 1984). Delcourt et al. (1983)

synthesized information from many such studies and depicted the relationships between perturbation, biotic response, and biotic patterning across a spectrum of time/space scales ranging from square meters and seconds to continents and millions of years (See Figure 1 in Holland, this issue) A current view is that landscape is a hierarchical mosaic composed of patches of various temporal and spatial domains that overlay one another (Hansen and Walker 1985, Urban et al. 1987) (Figure 1).

Ecotones as Boundaries Between Patches

The ecotone concept is closely aligned with the patch dynamics paradigm in that an ecotone can be thought of simply as a transition zone between adjacent patches. It is logical to expand the ecotone concept from its traditional form for application towards patches of any type or spatial scale. Accordingly, ecotone has been defined in 1987 by the SCOPE/MAB working group as a:

> *Zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems (Holland, this issue).*

The usage of "ecological system" here is analogous to that of "patch" above. Thus, ecotones may be between ecological systems of differing types and scales such as demes, populations, ecosystems, biomes, etc. (Holland, this issue). The reference to "strength of the interactions" stresses that ecotones are sites of exchanges of energy, materials, and organisms between patches. Recognition of the importance of interpatch flows and the role of ecotones in influencing these flows may considerably improve the predictive capability of the patch dynamics model. This topic is examined later in the section on ecological flows.

At present we are aware of no compelling arguments for differentiating between the terms "ecotone", "landscape boundary" and "transition zone". We

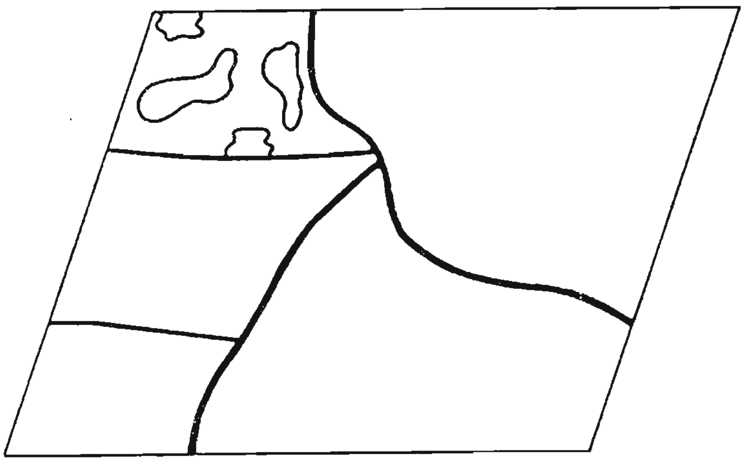

Figure 1. A landscape as a mosaic of patches of differing scale that overlay one another. This hypothetical landscape is composed of three major patches (e.g., soil types) (deliniated by heavy lines). One of these contains three meso-scale patches (medium lines). Several small patches lie on one of the meso-scale patches (e.g., soil turnover by mammals) (fine lines). From Hansen and Walker (1985).

use them here as synonyms. Regardless of what terminology is employed, it is important to keep in mind that boundaries are identifiable and meaningful only relative to specific questions and specific points of reference. What appears as an ecotone at one spatial scale may be seen as a collection of patches at a finer scale. And a structure that represents a barrier to one species may be optimal habitat to a second species and serve as a corridor for a third species.

Boundary Discreteness

Transition zones between patches in nature show a variety of forms. At a specific scale, some are abrupt disjunctions while others are broad and gentle gradients. At what point should an ecotone be called an ecocline or gradient? More importantly, do ecological properties differ between ecotones and ecoclines? Relatively few studies have addressed this topic.

Daubenmire (1968) recognized four general types of boundaries between plant communities:

1. abrupt transitions caused by discontinuities in an underlying environmental gradient;
2. gradual blending of vegetation due to smooth environmental gradients;
3. "mosaic" ecotones where peninsulas and islands of each community extend into the other, probably as a result of local heterogeneity in soil or microclimate;
4. sharp transitions even on smooth environmental gradients due to biotic interactions among organisms.

The first three are based on community distribution being closely related to controlling factors in the environment (e.g. soil moisture). Each is then distinguished by the abruptness and the degree of spatial heterogeneity within the ecotone. The fourth type is unique in having the control of environmental factors usurped by biotic interactions such as competition or mutualism (see also Armand 1985).

Daubenmire's approach was enriched theoretically by van der Maarel (1976) and empirically by Hobbs (1986). Building on van Leeuwen's work (1966), van der Maarel (1976) envisioned a continuum among hypothetical boundaries and described five types along the continuum based on abruptness of transition, degree of homogeneity within each adjacent patch, and extent of difference between the patches. He then predicted that each type has unique biotic structure and unique levels of species diversity.

This work is important because it raises the possibility of each ecotone type having unique ecological properties. Hobbs (1986) had only limited success in confirming these predictions with field data. Nonetheless, this effort to link ecotone pattern and ecological properties seems a profitable approach. A classification system based on, among other things, relative boundary width and heterogeneity may be important for developing theory on ecotones.

Ecotone Dynamics in Space and Time

It is important to recognize that ecotones are as ephemeral as the patches they separate. They may appear and disappear at one specific place. For example, an ecotone created by a lightning strike in a forest canopy may gradually disappear as the forest gap is filled by expansion of nearby canopy trees. Alternatively, ecotones may move across a landscape. Waves of early successional vegetation are known to move across some coniferous forests (Sprugel 1976) and some deserts (Boaler and Hodge 1962, Cornet et al. 1987). Clearly, all patches and ecotones are dynamic at some temporal scale. The motion of regeneration waves in fir (Abies) forests is visible over tens of years (Sprugel 1976). The responses of forest boundaries to glacial cycles is measured in thousands of years (Delcourt and Delcourt 1987) (Figure 2). The boundaries between tectonic plates fluctuate over tens of millions of years.

The concept of transition zones between patches that are spatially juxtaposed may be equally applicable to discontinuities in the state of one

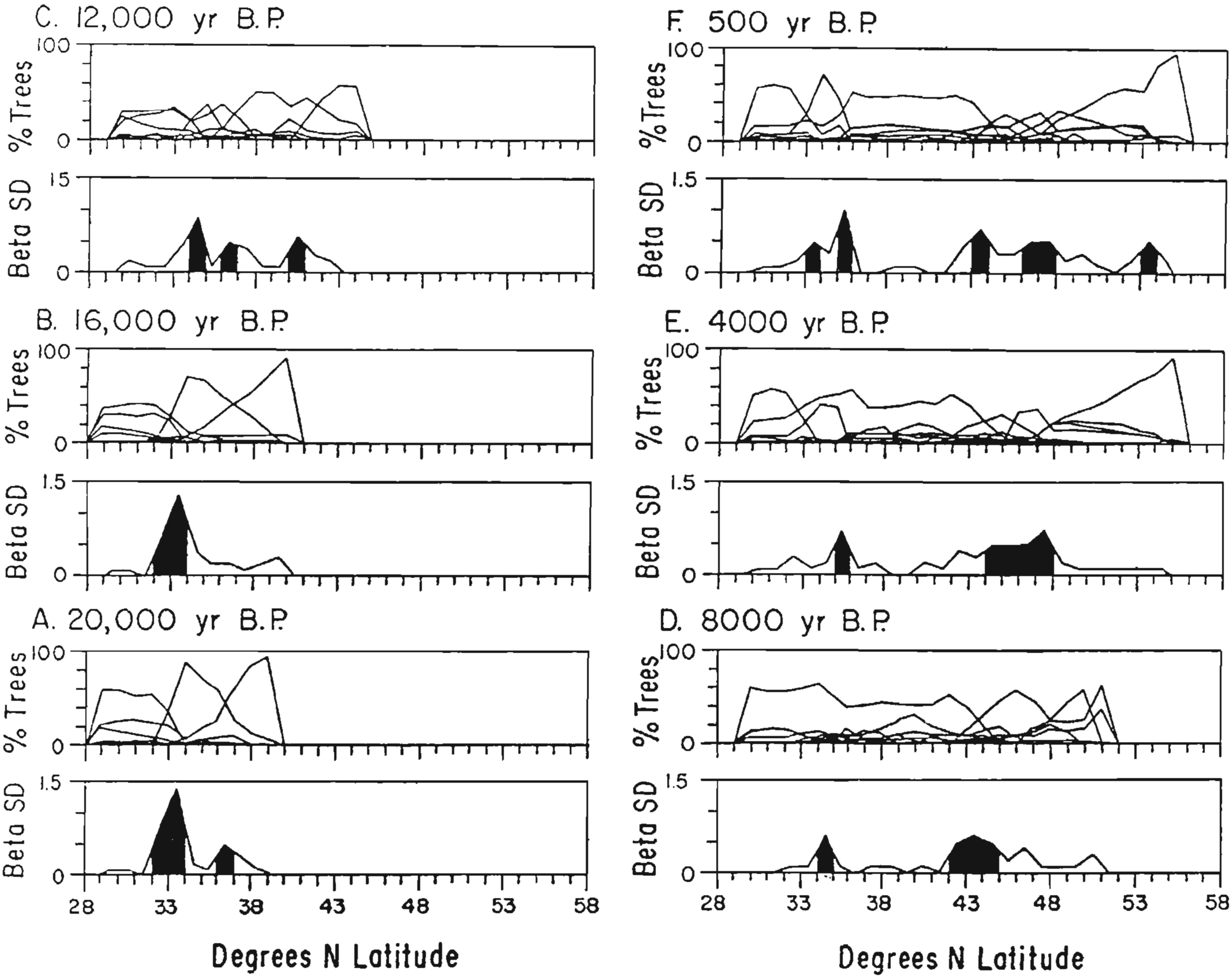

Figure 2. Late-Quaternary tree species dominance curves (upper panel) and latitudinal gradients in beta diversity (expressed as standard deviation) along a north/south transect at 85° w long. in eastern North America at: a) 20,000 years B.P.; b) 16,000 years B.P.; c) 12,000 years B.P.; d) 8,000 years B.P.; e) 4,000 years B.P.; f) 500 years B.P. The gradient is bounded by the Gulf of Mexico to the south to the north by tundra, glacial ice, proglacial lakes, or Hudson Bay. Tree dominance values are derived from pollen samples. Ecotones (black segments) are areas of high beta diversity as determinated by Detrended Correspondence Analysis. Modified from Delcourt and Delcourt (1987).

patch over time. Armand (1985) suggested, for example, that a timberline transition zone is a spatial analogue of vegetation change over time at a fixed location. A rich theoretical literature exists on thresholds in ecological system dynamics where a minor perturbation may push a relatively stable system to a new and very different state (May 1973, Walker et al. 1981). Exploring this concept of "ecotones in time" seems especially important now when human-induced climate change may cause rapid alteration of many components of the biosphere (Dyer et al. 1988).

Surficial Ecotones

Ecotones are typically envisioned as occuring perpendicular to the horizontal plane, separating patches positioned on the soil surface. Many landscape elements, however, are volumetric and have surficial boundaries with upper and lower strata as well as lateral boundaries with adjacent patches within the same stratum (Figure 5) (Johnston and Naiman 1987). The concept of volumetric patches or "patch bodies" is particularly applicable to ecological systems with pronounced vertical structure such as soil, aquatic, and forest systems. The dynamics of such systems may be strongly influenced by the characteristics of both the lateral and surficial boundaries or ecotones.

Examples of Ecotones

A few empirical examples will serve to illustrate ecotones of different types and scales. Figure 2 shows an ecotone between two major forest types lying along a north/south transect from the Gulf of Mexico to Hudson Bay in eastern North America 16,000 years B.P. (Delcourt and Delcourt 1987). The ecotone is defined by a relatively abrupt change in tree species composition that spans approximately two degrees of latitude (≈ 222 km).

A relatively small-scale ecotone between shrubland and grassland is depicted in Figure 3. This ecotone is deliniated by a relatively abrupt change in vegetative structure over a distance of approximately 55 m.

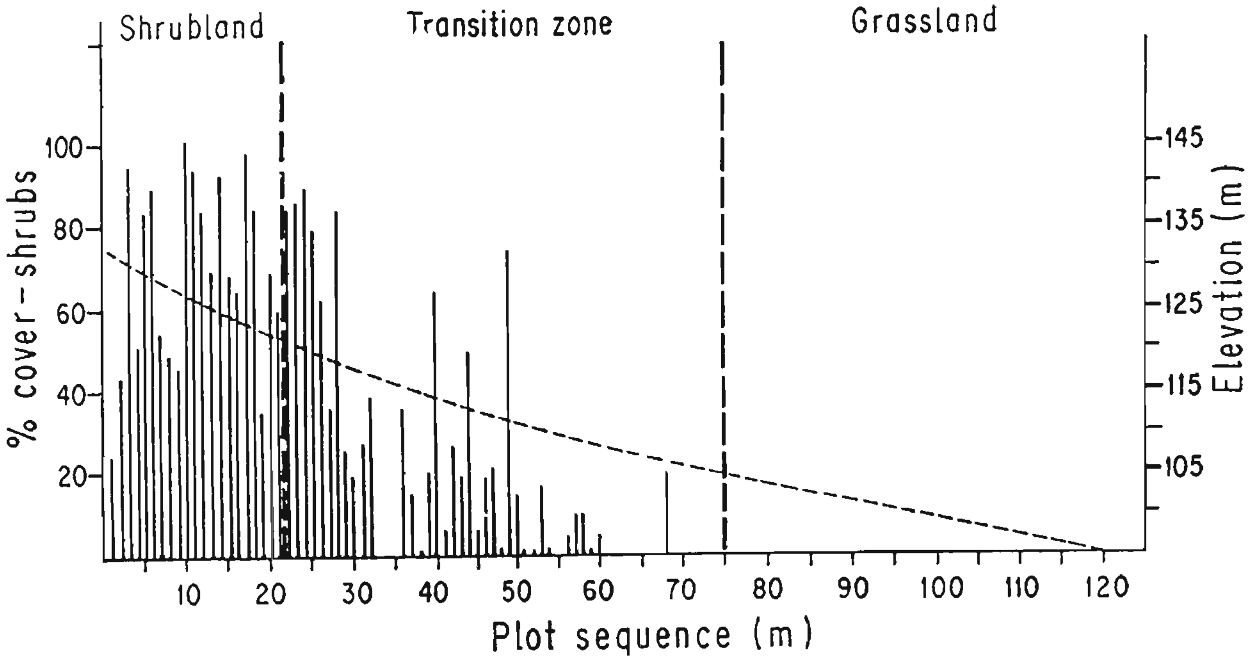

Figure 3. **Percent shrub cover (vertical lines) across a coastal sage scrub/grassland ecotone on Santa Cruz Island, California. The transition zone was identified by the classification procedure TWINSPAN. The horizontal dashed line denotes elevation. Modified from Hobbs (1986).**

The ecotone concept can also be applied to transition zones between populations with differing genetic structures. Figure 4 shows the frequencies of three different gene arrangements in Drosophila pseudoobscura along an east/west transect in the southwestern United States (Dobzhansky et al. 1977). The gradients of the chromosome frequencies are steep between coastal California and the arid intermountain zone and between the Rocky Mountains and Texas. These ecotones or "genotones" (C. Gliddon and P. Gouyon, personal communication) may serve as a basis for designating boundaries between races.

The Next Step

If the ecotone concept as defined by Clements (1905) was useful in understanding the distribution of plant communities in the early years of modern ecology, an expanded view of ecotones may enhance our understanding of ecological systems in the future. The concept may be applicable at a variety of spatial scales, to many types of ecological systems, to both lateral and surficial boundaries, and to discontinuities in time. A rigorous expansion of the concept requires the development and testing of formal research hypotheses.

WHY STUDY ECOTONES ?

What is to be gained by expanding the ecotone concept ? More generally, why study ecotones at all ? There are many answers that could be offered here (See other papers, this issue). We will examine three topics that are, in our opinion, among the most important reasons for further study on landscape boundaries. These are: (1) patch boundaries may influence ecological flows between patches; (2) unique patterns of biodiversity may occur in ecotones; and (3) human kind is substantially altering landscape boundary patterns without knowledge of the consequences. Our goal here is to focus attention on hypotheses and encourage further research, not to offer answers.

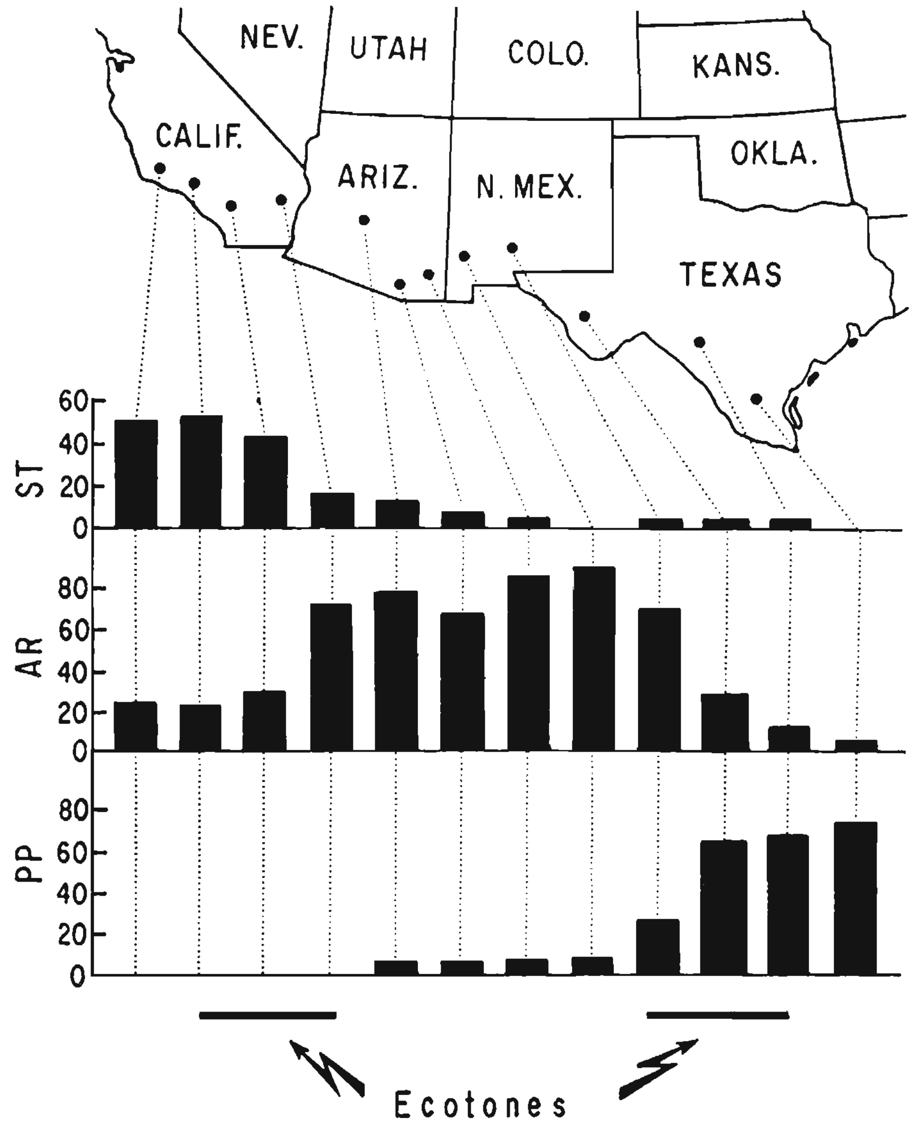

Figure 4. **Frequencies of three gene arrangements in third chromosomes of Drosophila pseudoobscura in the southwestern United States. Places where the gradients in chromosome frequencies are steep can be thought of as ecotones between genetic ecotypes. Modified from Dobshansky et al. (1977).**

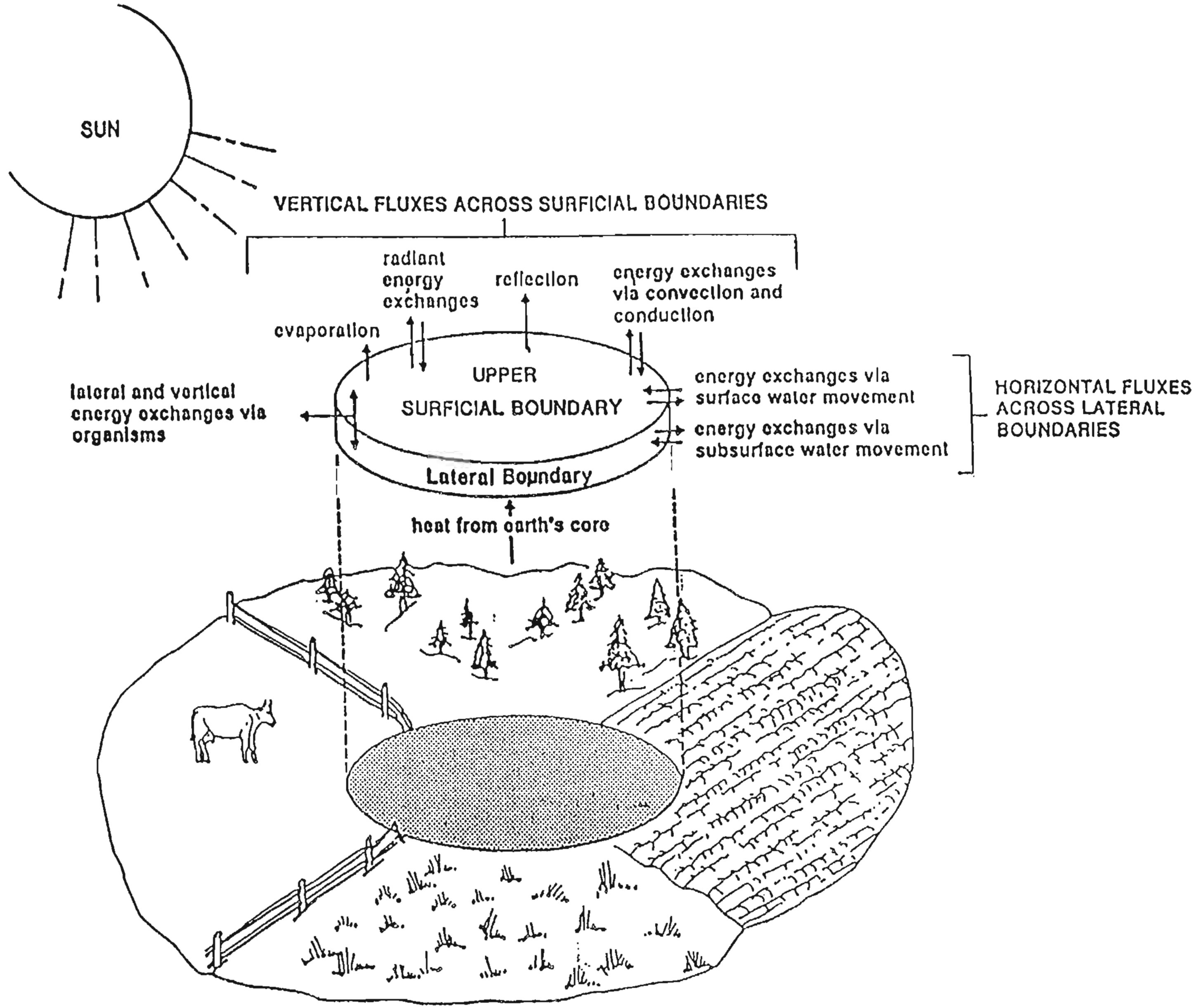

Figure 5. **A patch body extracted from a landscape mosaic, with associated energy fluxes. From Johnston and Naiman (1987), by permission of the International Association for Landscape Ecology.**

Patch Boundaries and Ecological Flows

The Importance of Interactions Between Ecological Systems

A central question in ecology has been, "How does the state of an ecological system at a given time influence the state of the system at some later time ?" A typical approach has been to view the system as internally homogeneous and isolated from other systems in order to focus on internal mechanisms of change. For example, many models on the dynamics of gene frequencies within populations assume no immigration or emmigration. The same is true for the exponential and logistic models of populations growth (Wilson and Bossert 1971). The approach has been especially important to the development of theory on ecological succession. The classical work of Clements (1936) described the interaction among the species, habitat, and climate of a place as the primary determinant of change in species composition. Migration of propagules into the system was acknowledged but other contagion effects from adjacent systems were not. The more recent facilitation, tolerance, and inhibition models of autogenic succession (Connell and Slatyer 1977) are based on species interactions within the designated system.

This approach has been productive but not sufficient to account for many of the patterns observed in nature. Natural systems are neither isolated nor homogeneous (Allen and Starr 1982, Pickett and White 1985). The patch dynamics paradigm (Pickett and White 1985) follows from the realization that ecological systems are heterogeneous and decomposable into many smaller-scale units. It focused attention on the extent to which landscape level dynamics can be predicted based on the aggregate behavior of many smaller-scale patches. Some widely-used forest dynamics models (Botkin et al. 1972, Shugart and West 1977) exemplify this approach. These models simulate the birth, growth, and death of individual trees on small plots (≈ 0.1 ha). The results from several plots are then averaged to describe the dynamics of the forest. These models have performed rather well in matching the dynamics of real forests (Shugart 1984) and this lends credence to the view that a landscape represents a simple aggregation of several independent patches. However, both hierarchy theory (Allen and Star 1982) and empirical observations (see below) suggest that consideration of contagion effects between patches will improve our understanding of landscape dynamics.

Hierarchy theory deals with the properties of systems that are composed of multiple levels and it is useful for exploring the organization of patchy systems. Many ecological systems appear to be organized as nested hierarchies with components at each level having unique spatial/temporal domains and properties (Allen and Star 1982, O'Neill et al. 1986, Urban et al. 1987) (Figure 6). Higher levels are generally larger in area than, behave more slowly than, constrain, and contain lower levels. Within a level of the hierarchy there may be several subsystems. These subsystems or holons (Koestler 1967) may be identified by the criterion that interactions within the holon are stronger than those with other holons, or by the criterion that there is greater similarity within the holon than between it and others (Allen et al. 1984). It is the interactions within and between the subsystems at one level that generate the behaviors of the next higher level. Conversely, higher levels in the hierarchy impose constraints that influence the dynamics of lower levels. To illustrate these ideas, consider a forest composed of trees and gaps. Trees interact and generate the dynamics of gaps. The structure of the canopy of a gap partially determines the microclimate on the forest floor and thus constrains the growth of individual seedlings. The important point here is that higher level properties are generated not only by interactions within holons at the next lower level, but also by interactions among those holons. Accordingly, we can improve our understanding of ecological systems by explicitly considering the contagion effects between components within the system.

In support of this notion, there is a wealth of empirical information indicating that the movements of energy, materials, and organisms across a landscape is influenced by the spatial distribution of the landscape elements. The spread of disturbances like fire may be enhanced by some

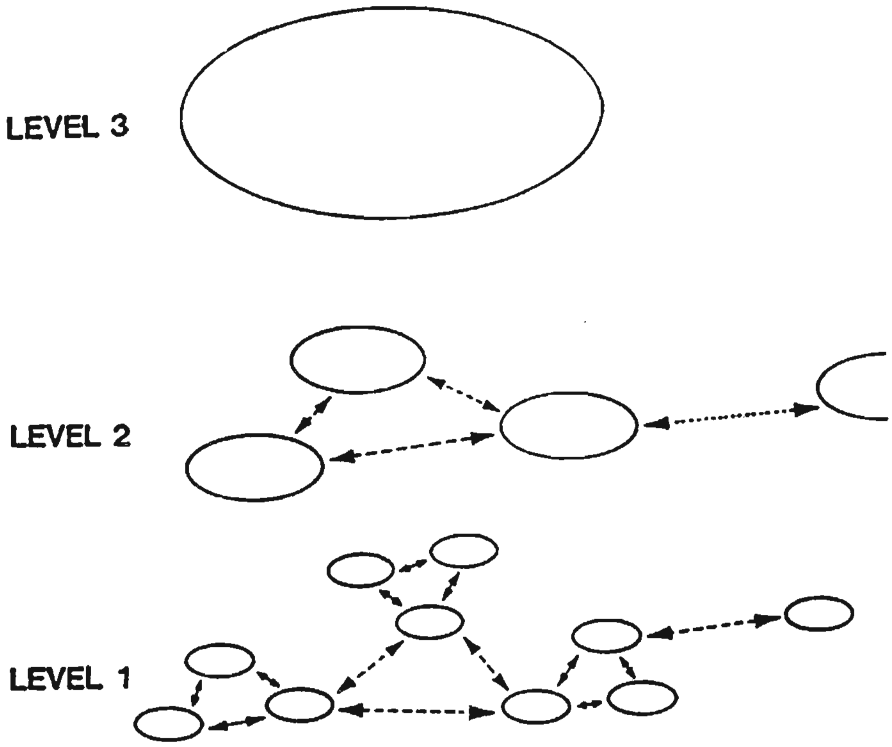

Figure 6. **A generalized hierarchical system. Thick arrows indicate strong interactions; broken arrows, weak interactions. From Urban et al. (1987), by permission of The University of Chicago Press.**

patch types and inhibited by others (Turner 1987). The microclimate or resource distribution within a patch may be modified by adjacent patches (Forman and Godron 1986). Colonization rates of animals or plants within a patch are often dependent upon the extent of connectivity of the patch with other similar patches (Fahrig and Merriam 1985).

These findings suggest that for predicting ecological dynamics, it is insufficient to know how the state of a system at a given time will influence the state at a future time. We must also know how the state of a system is influenced by the states of surrounding systems. A growing number of ecologists from diverse subdisciplines are investigating spatial effects. Ecotones should figure prominently in these studies.

Ecotones as Differentially-permeable Membranes

Interactions between elements of a landscape may be strongly influenced by the nature of the boundary between them. Returning to hierarchy theory, the surface of a subsystem represents a sharp discontinuity in the attribute that makes the holon a unique entity. This may be a change in structure, composition, or rates of processes (O'Neill et al. 1986). Holon surfaces may sometimes contain or encase the interactions within the holon or shield it from outside influences. The surface, thus, is analogous to a membrane that filters inputs and outputs and maintains the integrity of the holon. Similarly, the edges of a patch in a landscape are marked by a discontinuity in the attributes that define the patch. For example, a forest clearing is bounded by an abrupt increase in vegetation height. As stated earlier, an ecotone is the zone of discontinuity separating patches. In this regard, there is considerable interest in determining the extent to which ecotones act as differentially-permeable membranes that facilitate some ecological flows but impede others (Wiens et al. 1985, Johnston and Naiman 1987).

Materials, energy, and genetic information move across a landscape under the power of transport mechanisms or vectors (Wiens et al. 1985, Forman and

Godron 1986). Common vectors include wind, water, and organisms. The extent of movement is influenced by forces underlying the vectors. There are three general types of forces : diffusion, mass flow, and locomotion (Forman and Godron 1986). Diffusion is the gradual spreading of entities (e.g. molecules, organisms) as a result of random motion. Mass flow, such as of water or air, is powered by gravity or by temperature and pressure differences. Locomotion is the self-directed motion of organisms. Landscape boundaries may influence the strength and orientation of each of these forces.

Patch boundaries may sometimes act as barriers and impede the transit of disturbance, nutrients, or organisms. Coastal sand dunes, for example, are known to inhibit salt spraying and ocean flooding across islands (Odum et al. 1987). Dense hedgerows may reduce wind speeds over fields (Forman and Godron 1986) and probably inhibit the movements of wind-blown seeds or insects. Riparian forests retard erosion and down-slope movements of nitrogen and phosphorus (Peterjohn and Correll 1984). Strips of closely-cropped vegetation expose certain small mammals to high rates of predation and thus represent barriers to dispersal (Rice 1987).

Alternatively, landscape boundaries may be relatively porous to or even facilitate ecological flows across them. Wind blows freely through hedgerows that have an open structure. Beaver (Castor canadensis) easily traverse the boundary between aquatic and terrestrial systems, at least when surface ice is not present (Johnston and Naiman 1987). Patches with high fuel loads may enhance the spread of fire across a landscape (Turner and Bratton 1987). Strips of pioneer plants moving across relatively impermeable desert soils facilitate the flow of surface water into the soil and allow the establishment of a vegetation community (Cornet et al. 1987).

Finally, ecotones may serve as corridors or pathways and facilitate movements parallel to the patch edge. Some woodland birds have recently expanded their ranges across the North American prairie, probably by moving along riparian zones (Knopf 1986). Avian predators appear to aggregate in and move along habitat discontinuities (Gates and Gysel 1978). Similarily, riparian zones in the coniferous forests of the northwestern United States are thought to be used as movement corridors by many vertebrates (Harris 1984).

To summarize, the exchange of energy, materials, and genetic information between landscape elements appears to have an important influence on patch structure and function. Both theory and empirical evidence suggests that landscape boundaries sometimes act as differentially-permeable membranes and facilitate some ecological flows but impede others. The generality of this effect, the attributes of a boundary that cause it to repel or transmit ecological flows, and the consequences for landscape structure and functioning are poorly known and are fertile grounds for study.

Biodiversity in Ecotones

A reason for studying ecotones is that landscape boundary structure has a particularly strong influence on biotic diversity both because ecotones may serve as either barriers or corridors between gene pools and because ecotones represent unique habitats optimal for some species and inhospitable for others. These effects on biodiversity are evident at genetic, species, and landscape levels of organization.

The formation of a barrier to gene flow may subdivide a population into unique genotypes and, in some cases, lead to speciation (Mayr 1982). Landscape fragmentation following climatic fluctuations or disturbance is thought to be responsible for speciation in Pacific salmon (Oncorhynchus) (Neave 1958), Amazonian forest birds (Haffer 1969), and some new world warblers (Dendroica) (Mengel 1964).

When ecotones serve as habitat, they can strongly influence local and regional species density and diversity. A widely held tenet of wildlife biology is that the variety and density of organisms is elevated at the interface between plant communities (Leopold 1933). This "edge effect" is thought to be due to the presence of species characteristic of each of the adjacent communities plus species inhabiting only the ecotone. The edge specialists may find habitats at the ecotone that are not present in either community alone, or they may require two or more structurally different habitats in close proximity to one another (see Gates and Gysel 1978). The bald eagle (Haliaeetus leucocephalus), for example, forages along open bodies of water but requires large trees for nesting. Thus, breeding generally occurs along wooded shorelines (Hodges and Robards 1982).

Empirical studies of the edge effect are surprisingly few and concern primarily birds. Their results are sometimes contradictory and generally inconclusive. Weak evidence supporting the edge effect comes from comparisons of areas with mixed habitats (presumably with many edges) to areas of one habitat (Beecher 1942, Johnston and Odum 1956). More recent works focused directly on edges. Gates and Gysel (1978) and Chasko and Gates (1982) found that the species richness of nesting birds and nest density increased from forest interior to forest edge. In Kroodsma's (1982) study, however, nest density was highest near forest edges during only one of three seasons. Helle and Helle (1982) found that forest edges supported high bird densities, but lower species richness than forest interiors. Thus, clear trends on the generality of the edge effect do not emerge from these studies. Moreover, little is known about the environmental factors that might account for the patterns described above (see Kroodsma 1982, 1984).

A re-evaluation of theory concerning species diversity and abundance in ecotones appears to be necessary to better explain the patterns observed in nature. The increase in diversity in ecotones described by the edge effect is only one of some alternative possibilities. Van der Maarel (1976), for example, predicted that boundaries which fluctuate dramatically in location (as the edge of unstable water bodies) will be relatively poor in species. A reasonable way to expand theory on biodiversity at ecotones is to consider three possible levels of diversity in patch boundaries and evaluate the factors that could lead to each. Species diversity in an ecotone may be: (1) higher than in the adjacent patches; (2) intermediate between the patches; or (3) less than either patch. Below, we list a few speculative hypotheses to illustrate this type of approach.

The first scenario is described by the edge effect. As mentioned above, this situation exists if the ecotone supports species from each of the neighboring communities and/or edge specialists. Community overlap may be enhanced in ecotones where disturbance regimes or resource regimes intergrade or interdigitate in ways favorable to species from each community. For example, prairie fire may reach across the forest edge and create patches in the forest suitable for some prairie species. Alternatively, an ecotone may be relatively unfavorable but, nevertheless, contain many species if there are high rates of immigration from the adjacent communities. Ecotones may attract many edge specialists if they are of sufficient width, structure, and composition to comprise unique habitats or if the ecotone is bounded by two or more habitats that are necessary and sufficient for the edge specialists.

Ecotone diversity might be intermediate between two communities if one community is relatively poor in species and the ecotone supports only a portion of the species found in the richer community. The junction between an upland area and an inhospitable environment like a salt pan is a possible example.

In the third case, the boundary contains fewer species than either of the adjacent patches. This could result if the ecotone is subject to great fluctuations in resource levels (as in the saltwater/freshwater interface in estuaries) or experiences extreme levels of disturbance (e.g. the wave-battered region of the intertidal zone). Also, it is possible that the overlap of disturbances in an ecotone creates synergetic effects that are adverse to many species. Finally, edge specialists may be few if the ecotone is too narrow to provide a unique habitat.

This description of three patterns of diversity in ecotones is clearly underdeveloped. The main point here is that relatively unique conditions may occur at the interface of two or more patches and that these conditions may sometimes promote or inhibit species diversity. There is a need to develop predictions on the factors that influence biodiversity in patch boundaries and to test these predictions against patterns in nature.

Comparisons of diversity across landscapes need to control for differences in the spatial and temporal scales of the ecotones, patches and organisms being evaluated. For example, it seems unreasonable to compare diversity in a power-line corridor/forest ecotone to that in a prairie/forest ecotone because the former may be too narrow to serve as habitat for many species. Similarly, we need recognize that patterns of diversity on ecotones may differ between relatively large-scale organisms like large mammals and smaller-scale organisms like insects.

Lastly, there is a need for more consideration of the consequences of human alteration of landscape boundary structure on species diversity and abundance. Some surprising patterns have already been discovered. Gates and Gysel (1978) found that, whereas the density of nesting birds was highest on habitat edges, nesting success was lowest there due to increased predation rates. They suggested that narrow, man-made habitat edges may function as "ecological traps" by concentrating nests and thereby increasing density-dependent mortality. Also, there is increasing evidence that some patch interior species cannot tolerate habitat edges and become extinct in highly fragmented habitats (see Wilcove et al. 1986). Consequently, the strategy of maximizing local diversity by increasing the abundance of ecotones may lead to a reduction in regional diversity due to the loss of edge-avoiding species (Noss 1983).

Clearly, a great deal is yet to be learned about patterns of diversity and abundance at ecotones, controlling factors, and consequences for landscape structure and function. At a time when the loss of biotic diversity is a leading conservation problem (Wilson 1984), such studies are critical.

Human Kind and Ecotones

Human Impacts on Landscape Boundaries

Consideration of the role of ecotones in landscapes is especially important now because human activities are having unprecedented impacts on terrestrial and aquatic systems at the local, regional, and global levels (National Research Council 1986). In many places, human activities appear to be replacing natural agents of change as the primary determinants of landscape structure. Agricultural development, deforestation, and urban expansion have dramatically transformed upland and riparian vegetation and wildlife across continents (Cronon 1982, Burgess and Sharpe 1981, Swift 1984). In semi-arid areas, these activities have contributed to desertification and reductions in landscape productivity (Walls 1980). Man has also greatly accelerated the rate of species extinctions, especially in the tropics (Myers 1979, Ehrlich and Ehrlich 1982). And, there is a real concern that such changes will contribute to alterations in global climate (National Research Council 1986).

Natural disturbance is a common feature of all landscapes and plays a major role in driving patch dynamics (White 1979, Sousa 1984, Pickett and White 1985). Does human disturbance not represent more of the same ? In some cases the answer is no, and much work is yet to be done on the similarities and differences between natural and human disturbance.

A starting point is to classify agents of change by the ways that they influence ecological systems (Hansen and Walker 1985). Disturbance alters resources or organisms and causes a change of state. Non-events alter resources or organisms but do so at a scale insufficient to cause a change of state. And, incorporated disturbance alters resources or organisms in a way that is necessary to maintain the system in its present state. In the latter case, the component has adjusted to or "incorporated" a disturbance such that it now represents the status quo (Allen and Starr 1982). Plant species composition in the North American prairie is not changed by fire, it is maintained by fire (Allen and Starr 1982). Components of many ecological systems have over ecological or evolutionary time incorporated natural agents of change and are now dependent upon them (O'Neill et al. 1986).

The type of ecological response elicited by an agent of change is partially a function of the novelty of the event. New types of events will often represent disturbance because the system will not have previously adjusted to them. The relative spatial and temporal scale of an agent of change also influences its effects on an ecological system. According to the "scale hypothesis" (R. O'Neill, personal communication) events too small in scale to elicit response from the entity will be non-events (Figure 7). Also, large scale events that are relatively infrequent may be non-events if the biotic entity exists between pulses of the perturbation. Perturbations that are of sufficiently large scale to be agents of natural selection, but not so big or so intense or so frequent or so infrequent that the entity can not adapt to them will often be incorporated disturbance. Once the entity has adjusted to them, the events may be necessary to keep the entity in its present state. Perturbations at all other scales will usually be disturbance and cause a change of state in the entity.

Many human activities are similar in type or scale to natural events that have been incorporated by an ecological system. These activities may cause a change in the system only if they are discontinued. Other human activities, in contrast, differ either in scale or kind from natural agents of change (Urban et al. 1987). Humans sometimes rescale natural events. Fire suppression, for example, often results in less frequent but more intense fires than under natural conditions. Humans have also introduced new types of phenomena that are functionally similar to natural events but are of greater scale (e.g. timber harvest). Thirdly, humans have produced phenomena that have no natural counterparts (e.g. urbanization). Much of the biota is poorly adapted to these novel types and scales of phenomena. For this reason, the structure of natural landscapes often change markedly following the initiation of human activities.

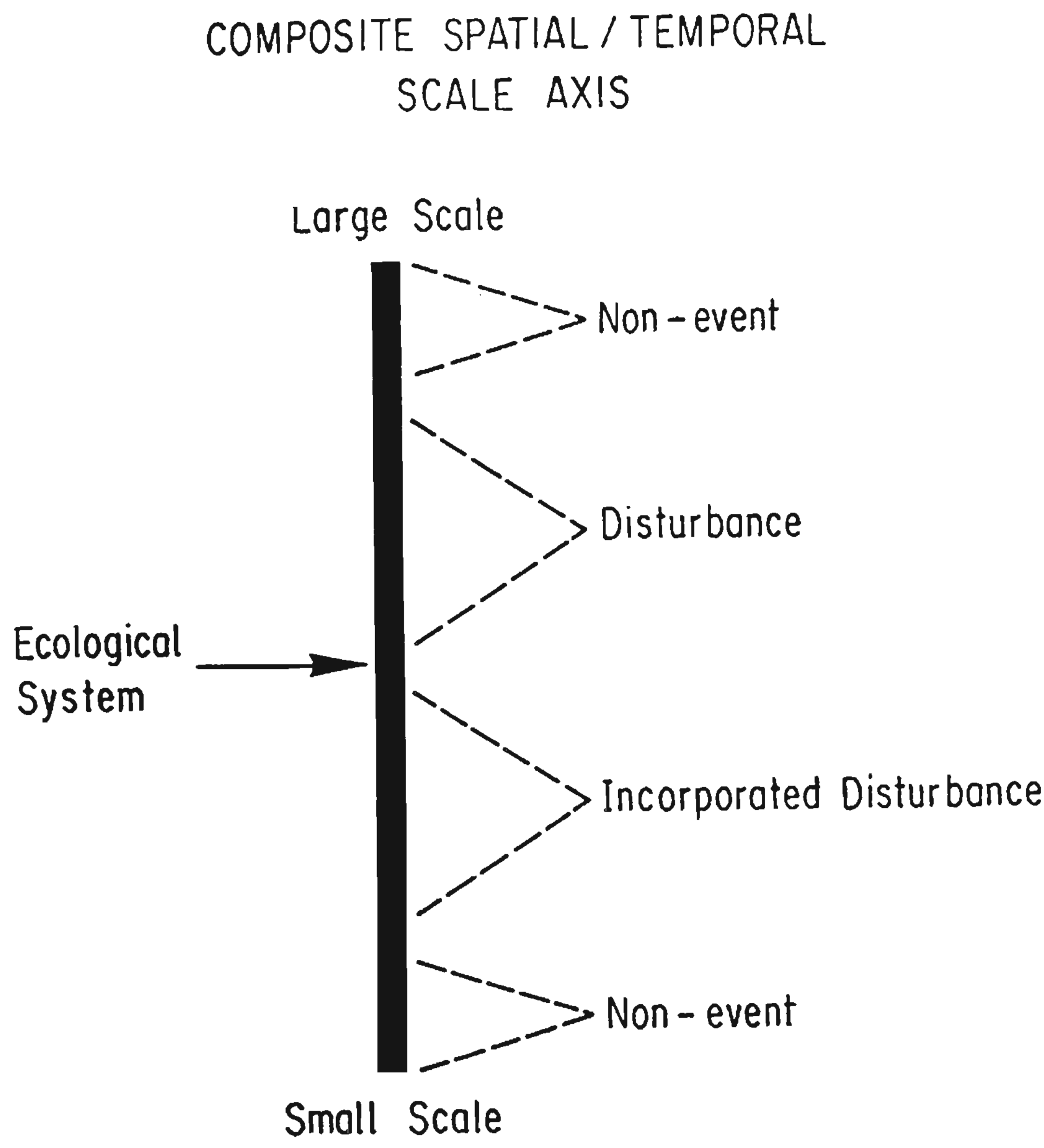

Figure 7. The response of an ecological system to an agent of change may be influenced by the spatial/temporal scale of the perturbation relative to that of the system. According to the model, events that are relatively small in scale or are extremely large in scale will not cause change in the ecological system, and are termed non-events. Events that are slightly smaller in scale than the ecological system may become "incorporated" by the system and be necessary to maintain the system in its present state. Moderately large scale events do cause change and are termed disturbance (R. O'Neill, personal communication). See text for further explanation.

Man's imprint on landscape structure has become ever more pronounced in recent years as human land use has broadened and intensified. Land transformation and other human activities appear to be initiating important changes in global climate (National Research Council 1986). These climatic alterations are expected, in turn, to induce further changes in terrestrial and aquatic systems (Dyer et . al. 1988). The emerging International Geosphere-Biosphere Program (IGBP) (National Research Council 1986) is designed to address these crucial problems.

Ecotonal areas are likely to be particularly susceptible to rapid changes in climate and atmosphere. Organisms in the transition zones between communities may be near their tolerance limits and thus be quick to respond to environmental change. For this reason, scientists involved with IGBP are interested in monitoring ecotones as early indicators of global change (see the other articles in this issue).

Ecotone Management

If landscape boundaries are important in influencing ecological flows and biodiversity, and human activities are dramatically altering these boundaries, then management actions are clearly desirable. One approach is to attempt to halt those human activities that have negative consequences. An alternative is to develop management strategies that mitigate the negative impacts. Unfortunately, little is known about how to manage landscape boundaries and an important reason for studying ecotones is to learn ways of producing desirable landscape patterns and characteristics. In places such as some wilderness areas a laisser faire approach may best accomplish management objectives. In other cases, land managers can capitalize on the human ability to alter landscapes and perform manipulations to acheive desirable patterns. Fire is commonly used in this regard. Prescribed burning is often designed to mimic natural wildfire regimes in order to maintain natural patterns. It is also used to produce novel patterns such as clearings for agriculture in tropical forests.

Perhaps, the most widely used technique relative to the manipulation of landscape boundaries is the creation of nedgerows. Hedgerow networks in agricultural areas greatly reduce soil erosion and provide a more equitable microclimate for crops (Forman and Godron 1986). Unfortunately, much less is known about managing boundaries in other types of ecological systems, especially in cases where management objectives are in conflict. The coniferous forests of the northwestern United States offer a typical example.

Managers of these forests are charged with maximizing timber production and maintaining viable populations of vertebrate species. This is difficult because some of the vertebrates require centuries-old forests (Franklin et al. 1981). These species are lost when the forests are managed on short (< 125 year) harvest cycles. Harris (1984) recently proposed a plan to solve the problem that is based on biogeography theory and landscape ecology. The core of the plan involves maintaining a network of old-growth patches and connecting corridors within a matrix of short-rotation forest. Successfully implementating the plan, however, would require more information on boundary dynamics. Presently, little is known about : how large the old-growth patches need be to prevent domination by edge effects; the types of vegetative corridors that would best facilitate animal movements ; the vulnerability of the patches and corridors to disturbances like fire and windthrow ; the extent to which nutrients and seeds would flow between the old-growth stands and the surrounding matrix. (Efforts to obtain this type of information are presently underway in Amazonian rain forests. See Lovejoy et al. 1986).

Our knowledge of boundary dynamics in these forests must be expanded in order to optimize management for timber production and for wildlife diversity. Similar types of resource conflicts exist in terrestrial and aquatic systems around the world. More research and creative management approaches are needed to maintain and produce desirable landscape patterns.

CONCLUSION

Returning to the question raised in the title -- "What and Why Ecotones ?" It is increasingly apparent that interactions between landscape elements strongly influence landscape function and structure. Ecotones represent the transition zones between landscape elements and may modify those interactions by acting as differentially-permeable membranes that influence the flows of energy, material, and organisms between patches. Ecotones may also be sites of high biotic diversity. Research on the validity of these hypotheses is certain to advance ecological theory and improve landscape management. The accelerating rate of human-induced changes in the biosphere necessitates that this research be given high priority.

ACKNOWLEDGEMENTS

Stimulating discussions and/or comments on the manuscript were provided by M. Dyer, C. Gliddon, M. Holland, B. Lacaze, J. Lepart, W. McComb, R. O'Neill, participants in the SCOPE/MAB Technical Consultation on Ecotones (see Holland 1988), and participants in the biweekly seminar series at the Centre Louis Emberger, C.N.R.S., Montpellier, France. This work was made possible by support from the Carnegie-Mellon Foundation and the Centre Louis Emberger, C.N.R.S., Montpellier, France. We offer thanks to all of these individuals and organizations.

LITERATURE CITED

Allen, T. E. H. and T. B. Starr. 1982. Hierarchy : Perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois, USA.

Allen, T. H. E., T. W. Hoekstra and R. V. O'Neill. 1984. Interlevel relations in ecological research and management: Some working principles from hierarchy theory. USDA Forest Service Gen. Tech. Rep. RM-110. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Armand A. D. 1985. The change of vegetation near the timber-line. Inter-Nord **17**: 59-62.

Beecher, W. J. 1942. Nesting birds and the vegetation substrate. Chicago Ornithological Society, Chicago, Illinois, USA.

Boaler, S. B. and C. A. H. Hodge. 1962. Vegetation stripes in Somaliland. J. Ecology **50**:465-474.

Botkin, D. B., J. F. Janak and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. J. Ecology **60**:849-872.

Burgess, R. L. and D. M. Sharpe, editors. 1981. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York, USA.

Carpenter, R. J. 1935. FLuctuations in biotic communities. 1. Prairie-forest ecotone of central Illinois. Ecology **16**:203-212.

Chasko, G. C. and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. Wildl. Monogr. **82**:1-41.

Clements, F. C. 1897. Peculiar zonal formations of the Great Plains. Am. Nat. **31**:968.

Clements, F. C. 1905. Research methods in ecology. University Publishing Co., Lincoln, Nebraska, USA.

Clements, F. C. 1936. Nature and structure of the climax. J. Ecology **24**:252-284.

Connell, J. H., R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. **11**:1119-44.

Cornet, A. F., J. P. Delhoume and C. Montana. 1987. Dynamics of striped vegetation patterns and water balance in the Chihuahuan Desert. Unpublished Communication at the International Symposium on Vegetation Structure. Utrecht, Netherlands.

Cronon, W. 1983. Changes in the land : Indians, colonists and the ecology of New England. Hill and Wang, New York, USA.

Curtis J. T. 1959. The vegetation of Wisconsin. The University of Wisconsin Press, Madison, Wisconsin, USA.

Daubenmire, R. 1968. Plant communties. Harper & Row, New York, New York, USA.

Delcourt, H. R., P. A. Delcourt and T. Webb III. 1983. Dynamic plant ecology: The spectrum of vegetation change in space and time. Quat. Sci. Rev. **1**:153-175.

Delcourt, P. A. and H. R. Delcourt. 1987. Long-term forest dynamics of the temperate zone. Springer-Verlag, New York, New York, USA.

Dobzhansky, T., F. J. Ayala, G. L. Stebbens and J. W. Valentine. 1977. Evolution. W. H. Freeman and Company, San Francisco, California, USA.

Dyer, M. I., F. di Castri and A. J. Hansen, editors. 1988. Geosphere-Biosphere Observatories: Their definition and design for studying global change. Biology International, Special Issue 16.

Ehrlich, P. R. and A. H. Ehrlich. 1981. Extinction: the causes and consequences of the disappearance of species. Random House, New York, New York, USA.

Fahrig, L. and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology **66**:1762-1768.

Forman, R. T. T. and M. Godron. 1986. Landscape ecology. John Wiley and Sons, New York, New York, USA.

Frankin, J. et al. 1981. Ecological characteristics of old-growth Douglas-fir forests. Gen. Tech. Rep. PNW-118. U.S.D.A., Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology **59**:871-883.

Griggs, R. F. 1914. Observations on the behavior of some species on the edges of their ranges. Bull. Torrey Bot. Club **41**:25-49.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science **165**:131-137.

Hansen, A. J. and B. H. Walker. 1985. The dynamic landscape: Perturbation, biotic response, biotic patterns. S. African Inst. Ecol. Bull. **4**:5-14.

Hansen, A. J., F. di Castri and P. G. Risser. 1988. A new SCOPE project. Ecotones in a changing environment: The theory and management of landscape boundaries. Biology International. Special Issue 17 : 137-163.

Harris, L. 1984. The fragmented forest. University of Chicago Press, Chicago, Illinois, USA.

Helle, E. and P. Helle. 1982. Edge effect on forest bird densities on offshore islands in the northern Gulf of Bothnia. Ann. Zool. Fennici **19**:165-169.

Hobbs, E. R. 1986. Characterizing the boundary between California annual grassland and Coastal sage scrub with differential profiles. Vegetatio **65**:115-126.

Hodges, J. I. and F. C. Robards. 1982. Observations of 3850 Bald Eagle nests in southest Alaska. Pages 37-116 in W.N. Ladd and P.F. Schempf, editors. Proceedings of the Raptor Management and Biology Symposium. Alaska Regional Office, United States Fish and Wildlife Service, Anchorage, Alaska, USA.

Holland, M., Compiler. 1988. SCOPE/MAB technical consultations on landscape boundaries. Report of a SCOPE/MAB workshop on ecotones. Biology International, Special Issue 17 : 47-106.

Johnston, C. A. and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1:47-57.

Johnston D. W. and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology **37**:50-62.

Knopf, F. L. 1986. Changing landscapes and the cosmopolitism of the eastern Colorado avifauna. Wildl. Soc. Bull. 14:132-142.

Koester, A. 1967. The ghost in the machine. MacMillan Publ., New York, New York, USA.

Kroodsma, R. L. 1982. Edge effect on breeding forest birds along a power-line corridor. J. Appl. Ecology **19**:361-370.

Kroodsma, R. L. 1984. Ecological factors associated with degree of edge effect in breeding birds. J. Wildl. Manage. **48**:418-425.

Le Cren, E. D. and R. H. Lowe-McConnell, editors. 1980. The functioning of freshwater ecosystems. IBP N° 22. Cambridge University Press, Cambridge, UK.

Leopold, A. 1933. Game management. Schriber, New York, New York, USA.

Livingston, B. E. 1903. The distribution of the upland societies of Kent County, Michigan. Bot. Gaz. **35**:36-55.

Lovejoy, T. et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 in M. E. Soulé, editor. Conservation biology. The science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

May, R. M. 1983. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Mayr, E. 1982. Speciation and macroevolution. Evolution **36**:1119-1132.

Mengel, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). The Living Bird **3**:9-43.

Myers, N. 1979. The sinking ark Pergamon Press, Oxford, UK.

Naiman, R. J., H. Décamps, J. Pastor and C. A. Johnston. 1988a. The potential importance of boundaries to fluvial ecosystems. Oikos. In Press.

Naiman, R. J., M. M. Holland, H. Décamps and P. G Risser. 1988b. A new UNESCO Programme: Research and management of land/inland water ecotones. Biology International, Special Issue 17 : 107-136.

National Research Council. 1986. Global change in the geosphere-biosphere. National Academy Press, Washington, D.C., USA.

Neave, F. 1958. The origin and speciation of Oncorhynchus. Trans. Royal Society of Canada. Series 3, Vol. 52, Sec. 5 pp. 25-40.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. BioScience. **33**:700-706.

Odum, E. P. 1971. Fundamentals of ecology, third edition. W.B. Saunders Company. Philadelphia, Pa.

Odum, W. E., T. J. Smith, R. Dolan. 1987. Suppression of natural disturbance: Long-term ecological change on the Outer Banks of North Carolina. Pages 123-135 in M. G. Turner, editor, Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.

O'Neill, R. V., D. L. De Angelis,J. B. Waide and T. F. H. Allen. 1986. A hierarchical concept of the ecosystem. Princeton University Press, Princeton New Jersey, USA.

Peterjohn, W. T. and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. Ecology 65: 1466-1475.

Pickett, S. T. A. and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., New York, New York, USA.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecol. Monogr. **45**:285-305.

Rice, K. J. 1987. Interaction of disturbance patch size and herbivory in *Erodium* colonization. Ecology **68**:1113-1116.

Shelford, V. E. 1913. Animal communities in temperate America. The University of Chicago Press, Chicago, Illinois, USA.

Shugart, H. H. 1984. A theory of forest dynamics: The ecological implications of forest succession models. Springer-Verlag, New York, New York, USA.

Shugart, H. H. and D. C. West. 1977. Development of an Appalachian deciduous forest succession model and its application to the assessment of the impact of the chestnut blight. Environ. Manage. **5**:161-179.

Sousa, W. 1984. The role of disturbance in natural communities. Ann. Rev. Ecol. System. **15**:535-591.

Sprugel D. G. 1976. Dynamic structure of wave-generated *Abies balsamea* forests in the northeastern United States. J. of Ecology 64: 889-891.

Swift. 1984. Status of riparian ecosystems in the United States. Water Research Bulletin 20:223-228.

Turner, M. G., editor. 1987. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.

Turner, M. G. and S. P. Bratton. 1987. Fire, grazing and the landscape heterogeneity of a Georgia Barrier Island. Pages 85-102 *in* M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.

Urban, D. L., R. V. O'Neill and H. H. Shugart. 1987. Landscape ecology : A hierarchical perspective can help scientists understand spatial patterns. BioScience **37**:119-127.

van Leeuwen, C. G. 1966. A relation of a theoretical approach to pattern and process in vegetation. Wentia **15**:25-410.

van der Maarel, E. 1976. On the establishment of plant community boundaries. Ber. Deutsch. Bot. Ges. Bd. **89**(5):415-443.

Walker, B. H., D. Ludwig, C. S. Hollings and R. M. Peterman. 1981. Stability of semi-arid grazing systems. J. Ecology **69**:473-498.

Walls, J. 1980. Land, man, and sand: Desertification and its solution. Macmillan Pubs., New York, New York, USA.

Watt, A. S. 1947. Pattern and process in the plant community. J. Ecol. **35**:1-22.

Weaver, J. E. and F. C. Clements. 1928. Plant Ecology. McGraw, New York, New York, USA.

Wiens, J. A., C. S. Crawford and J. R. Gosz. 1985. Boundary dynamics : A conceptual framework for studying landscape ecosystems. Oikos **45**:421-427.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. **45**:229-299.

Whittaker, R. H., and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. Theor. Popul. Biol. **12**:117-139.

Wilcove, D. S., C. H. McLellean and A. P. Dobson. 1986. Habitat fragmentation in the Temperate Zone. Pages 237-256 in M. Soulé, editor, Conservation biology: The science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, Massachusets, USA.

Wilson, E. O. 1984. Biophilia. Harvard University Press, Cambridge, Massachusets, USA.

Wilson, E. O. and W. H. Bossert. 1971. A primer of population biology, Sinauer Associates Inc., Sunderland, Massachusets, USA.

SCOPE/MAB TECHNICAL CONSULTATIONS ON LANDSCAPE BOUNDARIES

Report of a SCOPE/MAB Workshop on Ecotones
5-7 January 1987, Paris, France

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Abstract. Jointly sponsored by the International Council of Scientific Unions' Scientific Committee on Problems of the Environment (SCOPE) and Unesco's Man and the Biosphere Programme (MAB), a working group of eleven scientists gathered in Paris, 5-7 January 1987, to discuss the concept of ecotones. The technical consultation had triple origins. Recent discussions within SCOPE, MAB, and the developing Global Change Programme had centered on the need for a workable definition and classification of ecotones. Thus, the key objectives of the meeting were: (1) to develop a working definition of ecotones; (2) to prepare a classification scheme for ecotones based on operational concerns; and (3) to identify testable research questions.

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The group defined ecotone as a "Zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems".

Ecotones were classified based on mechanisms of origin and maintenance. In developing such a classification scheme, two approaches were used. One distinguishes between events that cause or maintain ecotones. The other approach involves the structure and function of ecotones themselves.

Seven central preliminary research questions were identified:

1. To what extent can ecotones be functionally classified so as to facilitate comparisons among different ecotones with respect to origin, structure and ecological processes?
2. Do ecotones provide stability for the resource patches they separate and, if so, at what spatial and temporal hierarchical scales do they operate?
3. What are the key attributes (processes and components) of ecotones which impart resistance and resilience of the adjacent resource patches to disturbance?
4. Is there a predictable pattern to dynamic change in ecotones under natural conditions?
5. How are the characteristics and processes of ecotones sensitive to changes in the global environment?
6. What is the importance of ecotones in maintaining local, regional and global biodiversity?
7. At what level of human investment have ecotones been maintained and restored in the past? Might that level be expected to continue, diminish or intensify in the future? At what scale are research results most useful for decision-making and management?

The SCOPE/MAB working session welcomed the suggestion that representative scientists from SCOPE participate in the initial planning and feasibility phase of the fledging MAB programme on the role of ecotones in aquatic landscape management and restoration. Likewise, the working group recommended that SCOPE establish a scientific advisory committee to direct a three-year data synthesis project on ecotones, and suggested that this SCOPE project be conducted in close co-operation with the MAB programme on ecotones and with the relevant programme development of IGBP.

INTRODUCTION

History of the Ecotone Concept

The notion of ecotones was used by Clements (1905) to denote the junction zone between two communities, where the processes of exchange or competition between neighbouring formations might be readily observed. More recently, E.P. Odum (1971, pg. 157) defined an ecotone as:

> *"A transition between two or more diverse communities as, for example, between forest and grassland or between a soft bottom and hard bottom marine community. It is a junction zone or tension belt which may have considerable linear extent but is narrower than the adjoining community areas themselves. The ecotonal community commonly contains many of the organisms of each of the overlapping communities and, in addition, organisms which are characteristic of and often restricted to the ecotone. Often, both the number of species and the population density of some of the species are greater in the ecotone than in the communities flanking it. This tendency for increased variety and density at community junctions is known as the edge effect".*

Two points of view have developed on the concept of ecotones. One has placed an emphasis on genetic and species diversity (Schonewald-Cox et al. 1983, Patten et al. 1985, Rusek 1986) and involves exchange of genetic materials between different populations; interactions between species including predation (Bartholomew 1970, Quinn 1986), dispersal (Acherar et al. 1984, Debussche et al. 1985), and allelopathy (Muller and del Moral

1971); consequences at the population level such as genetic differentiation; and consequences at the community level (Bellamy et al. 1969, Roth 1976, Strelke and Dickson 1980). The second approach has emphasized the cycling of materials and the flow of energy (Peterjohn and Correll 1984, Shugart 1984) and environmental modifications (Boaler and Hodge 1962, White 1971, Reiners and Lang 1979, Tranquillini 1983). In some cases the two approaches have been linked (Davis and Mooney 1985).

Few general theories have been prepared. The most comprehensive theory - that of van Leeuwen (1966) (see also van Leeuwen and van der Maarel 1971, van der Maarel 1976) - offers a scheme for classifying ecological boundaries and describes the general properties of each type. Although this work is speculative, some ecologists (Margalef 1979, Hobbs 1986) use it as a framework in their studies of the boundary between vegetation units. A number of elements of the concept have been borrowed from Watt's (1947) ideas on "pattern and process", from Levin and Paine's (1974) notion of patches, and more generally from the development of successional theory (Clements 1916, Drury and Nisbet 1973, Connell and Slayter 1977).

Background for Technical Consultations

Given the lack of general acceptance of a single theory on the concept of ecotones, a discussion of the topic was held in early 1987. Organized jointly by the International Council of Scientific Unions' (ICSU) Scientific Committee on Problems of the Environment (SCOPE) and Unesco's Man and the Biosphere Programme (MAB), a technical consultation on the concept of ecotones took place 5-7 January 1987 at ICSU headquarters in Paris, France. A list of the scientists who participated in this consultation is given in Annex I.

Interest of Organizations in Programmes of Ecotones

The technical consultation had triple origins. Recent discussion within SCOPE, MAB, and the developing Global Change programme (International Geosphere-Biosphere Programme or IGBP) had centered on the need for a workable definition and classification of ecotones (Holland 1986).

SCOPE. The Sixth General Assembly of SCOPE met 9-13 September 1985, in Washington, D.C., USA, noted the fundamental worldwide importance of ecotones and the paucity of synthesized information on them, and recommended that SCOPE establish a small ad hoc committee to develop as soon as possible a new proposal on ecotones. At the 19th meeting of the SCOPE Executive Committee, held in Nairobi, Kenya, on 10-11 May 1986, F. di Castri reported on his enquiry on the feasibility of an ecotones project. The Executive Committee invited him to convene a small ad hoc group to prepare a detailed proposal for a study focusing on the role of ecotones as indicators of change. Also in May 1986, a National SCOPE Conference "Ecotones - Resources of the Genetical Diversity of Organisms" was organized by the Czechoslovak National Committee (CNC) for SCOPE and by the Institute of Soil Biology of the Czechoslovak Academy of Sciences at Ceske Budejovice (CSSR). The objective of the conference was to review the state of knowledge on ecotone problems and to stimulate further research. Three groups of papers were presented: (1) botanical contributions, (2) contributions from a soil biological investigation of a classical meadow-spruce forest ecotones, and (3) contributions on vertebrates and invertebrates in the ecotones (Rusek 1986). These events led to the present SCOPE project on landscape boundaries (Hansen et al., this issue).

MAB. A workshop on Land Use Impacts on Aquatic Ecosystems: The Use of Scientific Information " was held 21-25 April 1986 in Toulouse, France. Jointly sponsored by Unesco MAB-5 and the Centre National de la Recherche Scientifique (CNRS), the outcome of this workshop was the realization of the crucial role ecotones play in regulating transient biogeochemical processes and the character of the landscape mosaic. It was agreed by the assembly to focus the MAB-5 working group on an intense examination of the role of ecotones, their management, and their restoration. The overall objective of the MAB programme is to develop a predictive capability for understanding the role of boundaries (ecotones) in determining landscape patterns and ecological processes (Naiman 1986, Naiman et al., this issue). This understanding will be used to develop a rational management plan for conservation of ecotones and for use in addressing detrimental environmental practices.

GLOBAL CHANGE. The report from a workshop entitled "Spatial and Temporal Variability of Biospheric and Geospheric Processes: Research Needed to Determine Interactions with Global Environmental Change" notes that global change is frequently caused by an aggregation of local and regional changes at critical points in space and time (Risser 1985). For example, in the interactions between land and water, water movement is a primary factor determining terrestrial and aquatic biotic processes. From the perspective of Global Change, the overall scope of the land-water interface problem suggests three primary objectives. The first is defining bioclimatic zones that identify relatively homogeneous land surface regions and the potential changes in the biota-water-landform interactions. Second, a paradigm must be developed that can address changes in the movement of water and materials within and between these bioclimatic zones. Finally, a quantitative basis for analyzing the changes in variables such as primary production, fish yield, and physical structures in the estuarine and nearshore coastal waters should be developed.

Current understanding and technologies address components of this complex task, but the ability to synthesize the relevant information on a set of larger and consistent scales is lacking. On a purely theoretical basis, it is currently very difficult to identify a set of guiding principles or rules that will uniformly permit the matching of temporal and spatial scales from the wide range of scientific disciplines involved in answering questions about the important biospheric problems facing the world today (Risser 1985). Hierarchy theory seems to offer some points of departure toward answering these questions, but the current state of knowledge suggests that these rules may be question-specific. If questions about matching scales can be answered only on the basis of the specific question being addressed, then the proper analytical approach is to attempt to explicate the scaling issue within the context of important biospheric issues (Risser 1985).

General Objectives for Technical Consultations

Given the agreement among members of the international scientific community as to the importance of increasing scientific knowledge on ecotones, the SCOPE/MAB working group was assembled in January 1987 to review information on ecotones, and identify major gaps. Three overall objectives for the meeting were: (1) to develop a working definition of ecotones; (2) to prepare a classification scheme for ecotones based on operational concerns; and (3) to identify testable research questions. These consultations provided an opportunity for examining steps for the further development of the MAB project on ecotones. They also resulted in a series of recommendations on possible SCOPE activities on ecotones, accepted by an expanded session of the Executive Committee of SCOPE, in Bangkok in February 1987. Also discussed were possible avenues for co-operation between MAB and SCOPE with respect to ecotones, as well as potential links with ICSU's International Geosphere-Biosphere Programme.

The purpose of this report is to summarize the discussions of the SCOPE/MAB working group on ecotones. The reader should bear in mind that the workshop represented, more or less, a "brain-storming" effort among the participants. Many of the ideas included in this report are preliminary and undeveloped. They are presented in an effort to stimulate discussion and further research. This report first examines linkages between ecotones and patch dynamics theory, derives a definition for ecotones, and presents schemes for classifying ecotones. Then, the possibility of monitoring landscape boundaries for assessing changes in global variables is discussed. Finally, questions for future research and recommendations are presented.

ECOTONES AND PATCH DYNAMICS

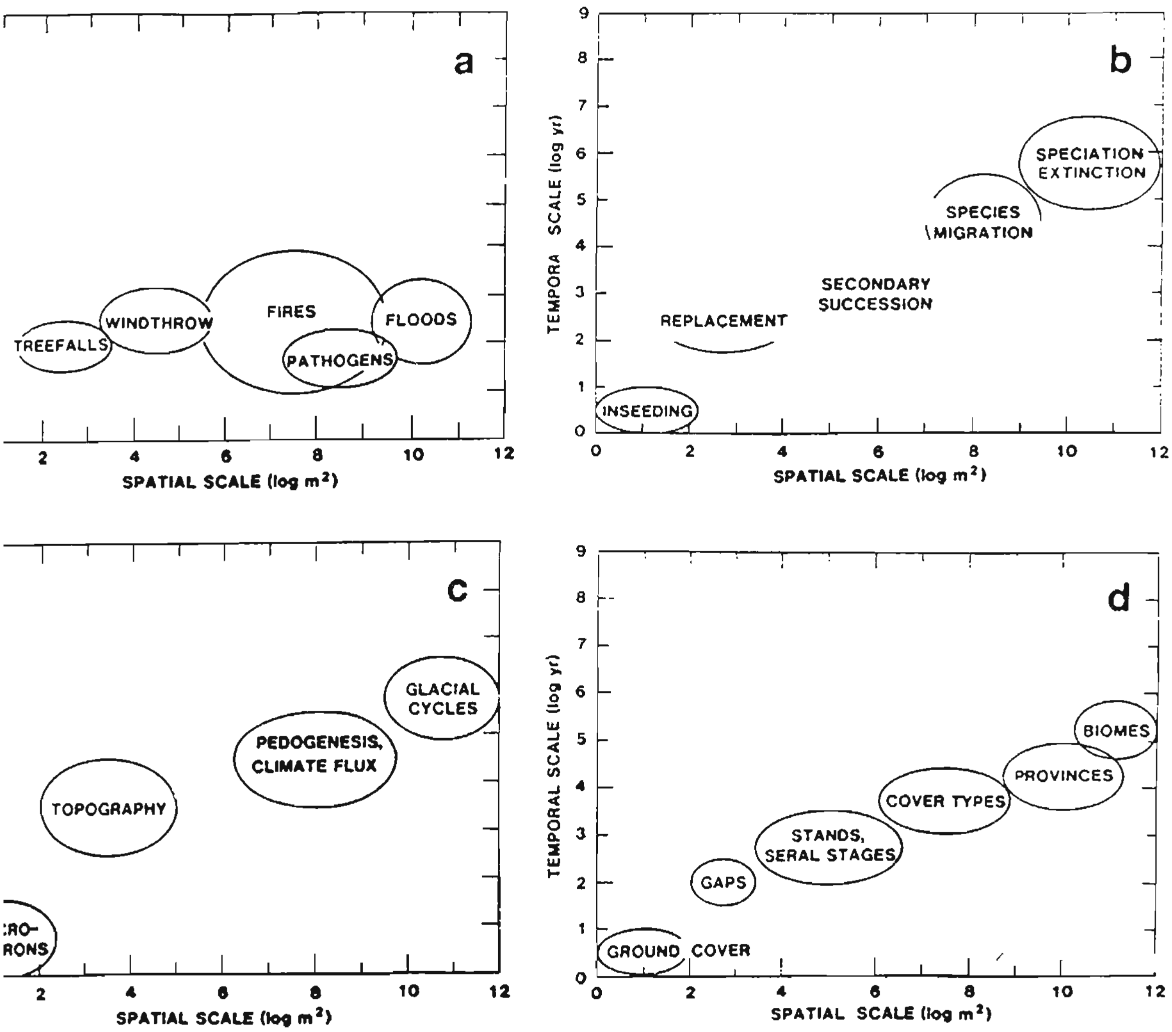
Ecologists have long realized that most ecological systems are composed of several distinct components and are thus heterogeneous. Clements (1936) described the patch structure of vegetation at several different spatial scales. Watt (1947) expanded on this approach by considering patch turnover in time as well as space. The concept of "patch dynamics" is now well developed and landscapes are widely viewed as mosaics of patches that have unique properties and function at differing rates (See Pickett and White 1985, for a review). Ecotones are simply boundaries between patches and, thus, are prominent features of heterogeneous ecological systems.

The forces that create and destroy patches and ecotones in landscapes include disturbance, biotic processes, and environmental constraints (Levin 1978). These agents occur at a variety of spatial and temporal scales (Figure 1). As elucidated by Urban et al. (1987, pg. 119):

> *"Disturbances range from the localized effects of an individual death to the large-scale effects of wildfires, drought, and epidemic disease. Biotic, or regenerative, processes also vary in scale from the regrowth of an individual to the reorganization of species assemblages. Environmental constraints include microclimatic and fine-scale soil conditions governing seed germination, and also subcontinental climatic regimes that delineate biomes, such as the Eastern Deciduous Forest."*

This perspective seems useful for understanding several types of ecological systems. Inherent in this view is that ecotones occur at a variety of spatial and temporal scales (van der Maarel 1976) and have properties that are, at least partially, scale dependent.

From an evolutionary point of view, ecotones have been thought to be important for the origin (Mayr 1982, Vruba 1985) and survival (Diamond and May 1981, Jenik 1983) of biotic species. With the retreat of the ice-sheets during the Holocene, changing climates allowed many plants to expand their



re 1. (a) Disturbance regimes, (b) forest processes, (c) environmental constraints, and (d) vegetation patterns, viewed in the context of space-time domains. Modified from Delcourt et al. (1983). From Urban et al. (1987), by permission of the American Institute of Biological Sciences.

ranges northwards (Davis 1981 and 1983, Huntley and Birks 1983). In some cases, vegetation assemblages have been accurately reconstructed through studies in space and time, and changes have been analyzed as ecotone dynamics (Grimm 1983). Studies of tree population demography have allowed analyses of the consequences of small climatic fluctuations on mountainside tree lines (Payette and Filion 1985, Kullman 1986).

In addition to the more obvious spatio-temporal mosaics that occur at the landscape/community level, there can also exist substantial heterogeneity within species and populations. This heterogeneity is often manifest at the level of physiologically and/or genetically distinct groups, each of which itself appears homogeneous when viewed at the community level. For example, McNeilly (1968) looked at the community within and surrounding a small copper mine in North Wales, U.K. The area inside the mine boundary is heavily polluted by mine spoil with very little plant cover. There is a sharp boundary across which the toxic waste is replaced by permanent pastures growing on unpolluted soils. The mine boundary clearly is an ecotone separating two distinct communities. One grass, Agrostis tenuis, transcends the ecotone but has genetically distinct ecotypes in each community. In the ecotone both genetic variants are found due to a limited exchange of genes via sexual reproduction and seed dispersal in the two "populations".

The functioning of an ecotone influences both the internal properties of the ecotone, and the properties of adjacent patches. Boundaries are often locations where the rates of ecological transfers change abruptly in relation to those within patches (Wiens et al. 1985). Hence, ecotones can be thought of as patches having properties that differ from other system components. They are, for example, often particularly rich in resources, support high productivity, and are structurally variable (Forman and Godron 1986). These features partially explain why producers and consumers are abundant and diverse in ecotones. Ecotones influence adjacent patches by exerting control over ecological transfers. Wiens et al. (1985) likened boundaries to the membranes of organisms in that they vary in permeability or resistence to flows of energy, materials, organisms, and information. For example, fields separating woodlots may act as barriers to the dispersal of small mammals (Wegner and Merriam 1979). Also, disturbance events that disrupt patches may be either dampened or promoted by ecotones (Forman and Godron 1986). Additional studies of ecotone properties and their influences on patch function and structure will undoubtedly improve our understanding of ecological systems.

Humans, of course, have played a major role in driving the dynamics of many landscapes (Barker 1985, Delcourt 1987). Some human activities may mimic natural disturbances and be of little concern ; others are unique in kind or scale and, consequently, have dramatic repercussions (Urban et al. 1987). Greek and Latin civilizations brought about forest destruction in the circum-Mediterranean area (Thirgood 1981, Meiggs 1982). Similarly, human land use practices along the sub-humid/humid transition zone in Africa have strongly influenced the location of the savanna/forest boundary (Hopkins 1983). Human activities sometimes reduce landscape heterogeneity. For example, stream channelization often reduces the number of ecotones in a river valley (Johnston et al. 1982, Holland and Burk 1984, Sedell and Frogatt 1984) (Figure 2). Likewise, intense deforestation may lead to a reduction in the number and length of grassland/forest ecotones (Darby 1956, Bosson-Lamouille et al. 1980, Bouchet et al. 1980, Burgess and Sharpe 1981) (Figure 3). Conversely, low to moderate levels of forest fragmentation (Curtis 1956, Burgess and Sharpe 1981, Whitford 1983) may increase the number of ecotones present. Consideration of the unique effects of some human activities on landscape dynamics is essential to the study of ecotones.

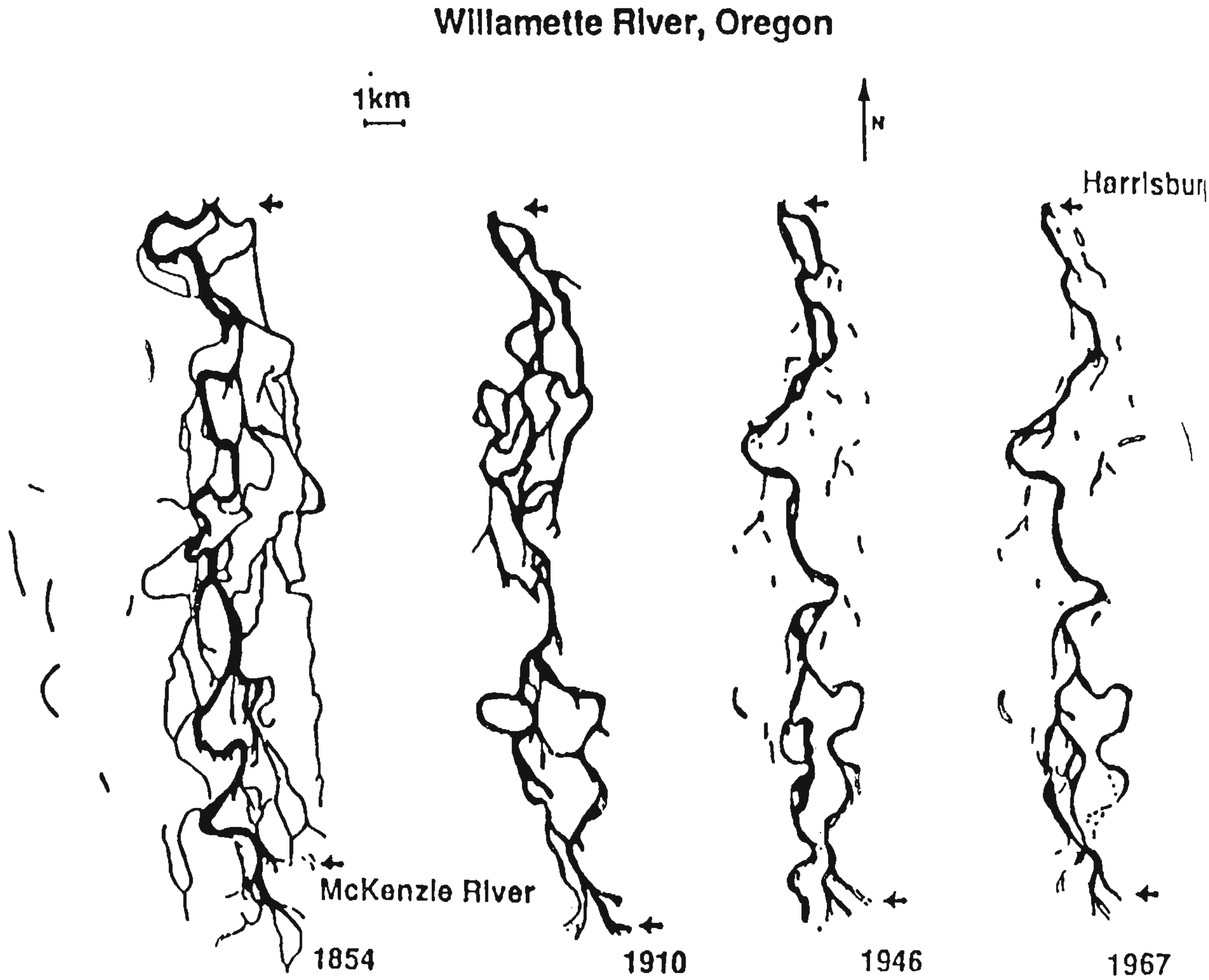


Figure 2. **The Willamette River, Oregon, USA, from the McKenzie River confluence to Harrisburg, showing reduction of multiple channels and loss of shoreline 1854-1967. From Sedell and Frogatt (1984), by permission of E. Schweizerbart'sche Verlags buchhand lung (Stuttgart).**

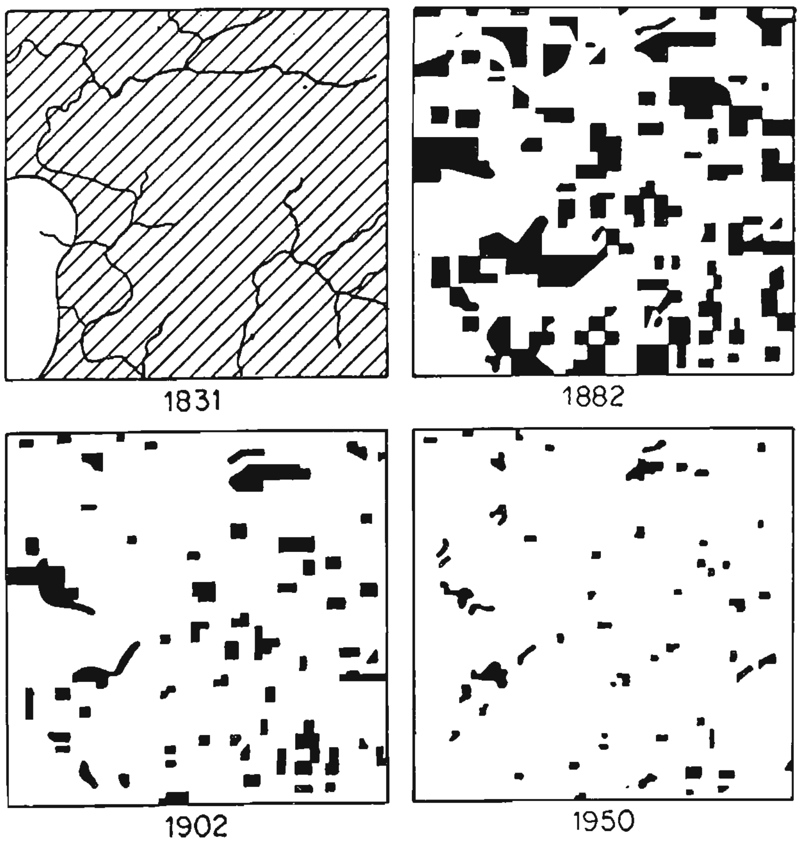


Figure 3. **Changes in wooded area of Cadiz Township, Green County, Wisconsin, during the period of European settlement. The shaded areas represent the land remaining in, or reverting to, forest in 1882, 1902, and 1950. From Curtis 1956, by permission of the University of Chicago Press.**

DEFINITION

The working group developed the following definition of ecotones based on operational concerns:

> *Zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems.*

The term "ecological systems" is meant to include commonly described hierarchical entities such as demes, populations, communities, ecosystems, landscapes and biomes. Thus, ecotones can be described as transitional zones between ecosystems, or between biomes, etc. Ecotones possess specific abiotic and biotic characteristics, such as physical and chemical attributes, biotic properties, and energy and material flow processes. These characteristics are also used in defining ecosystems and biomes, but the unique conditions of ecotones are the interactions with adjacent ecological systems. Some ecological flows across ecotones may be unidirectional, moving only from one patch to another, while others are bidirectional. The strength of these interactions, which may vary over time and space scales, may be driven by the contrast between adjacent ecological units (i.e., the distinctions among the characteristics and the dynamics of the relevant processes within the adjacent ecological systems and the ecotone itself).

This working definition is different from that of Odum (1971) (See Introduction) in its consideration of space and time scales as well as in its attention to "the strength of the interactions between adjacent ecological systems". Members of the Technical Consultation recognize that their working definition is relatively general. However, the scientists assembled agreed to such a general definition as a launching point for development of the theoretical base necessary for future discussions (by SCOPE, MAB and IGBP) of the ecotone concept.

RATIONALE

The simultaneous call for study of ecotones by SCOPE, MAB and IGBP suggests the widespread recognition of the importance of ecotones. This importance is based on four suppositions: the number of putative characteristics of ecotones that are significant in understanding ecological systems in general; the assumption that ecotones are highly susceptible, and are thus good early indicators of changes; the potential significance of ecotones for prudently managing the biosphere; and the recognized relative paucity of data from ecotones.

Studies of ecotones have been undertaken, but few general theories about ecotones have been prepared. Historically, studies of ecological systems have concentrated on the internal portions of relatively homogenous sites, and few investigations have focused on the boundary of transitional sites (Le Cren and Lowe-McConnel 1980). Thus, there is a comparative lack of data from ecotones, and, furthermore, comparatively few techniques exist for explicitly measuring the dynamic processes characteristic of ecotones. General understanding of the principles applicable to ecotones will depend upon the collection and interpretation of data from ecotones throughout the world. Likewise, there is a need for better statistical studies of gradients and time-series analyses.

It is difficult to adequately describe the dynamics of any ecological system without delineating the boundary conditions. In order to provide a quantitative scheme, it becomes important for ecology to follow explicit mathematical rules; that is, solutions to problems depend upon stating boundary conditions. Modellers already do follow explicit mathematical rules; however, in general, mathematical rules are not always followed for more empirical field studies.

Despite the relative paucity of data, there are a number of charateristics of ecotones thought to be important in understanding ecological systems. Examples of characteristics of some ecotones include the following:

elevated abundance of resources; important control points of energy and material pathways (Peterjohn and Correll 1984); potentially sensitive sites for studying the interactions of biological populations and their controlling variables; support of relatively high biological diversity (Patten et al. 1985); maintenance of critical habitats for a number of species (Johnston and Odum 1956); and refuge and source region for agricultural pests and predators. Other characteristics which may be specific to a particular type of ecotone include : sites for longitudinal migration (e.g. windbreaks), influence on climatic regime of the surrounding area/soil conditions (e.g. forest/grasslands ecotones), and genetic pool for surrounding ecological systems and sites for active micro-evolution (e.g. forest/agricultural field ecotone).

In part because of these characteristics, ecotones are potentially important in the judicious management of the biosphere. If, for example, ecotones prove to be effective controls in the movement of nitrogen, phosphorous and other material across the landscape, then management of the ecotones will be instrumental in determining the locations of these materials in terrestrial and aquatic environments (Wiens et al. 1985, Pinay 1986, Johnston and Naiman 1987). Similarly, if ecotones harbour a particularly large number of species, then ecotones become very important in managing the biodiversity of the biosphere.

While in the past work has been undertaken on the identification of ecotones, scientists now agree that there is a need to look at changes over time. As lines of transition (or boundaries), ecotones often appear very clearly on satellite imagery (Gonzales and Casanova 1987). Therefore, during the last several years, remote sensing has proven to be a useful tool in identification of ecotones throughout the world. White and MacKenzie (1986) present a detailed analysis of the manner in which high resolution remote sensing approaches can be coupled to detailed knowledge of vegetation distribution and community processes on the ground. Dyer and Crossley (1986) warn that although there is little doubt about the need for a major programme coupling remote sensing and ecology, it is not entirely clear how such a programme should be constructed because interconnections between the diverse disciplines are tenuous. Thus, a monitoring programme designed specifically for ecotones, taking into account the specific characteristics of zones under study and the continuing progress on technology development for remote sensing, has yet to be launched.

Humans have a substantial economic and ecological investment in ecotones. For instance, windbreaks are thought to be economically valuable: they modify the air temperature or humidity of the soil in a positive or negative way depending on their position and according to the environment (SCOPE 1986). As cultivation and civilization expand there are concomitant changes in the ratios of edge to surface area and patch volume (Johnston and Naiman 1987). This change is proceeding without sufficient information on the biotic implication of such change.

Natural resource managers need to consider the role of ecotones in conjunction with a variety of other factors. However, ecotones have practical implications for the management of natural environments, including:

- Ecotones play an important role in regard to predation phenomena and (in general) in biological control. They constitute a refuge zone for certain depredators of trees; they can also be "reservoirs" for parasites of crop pests;
- The reproduction of many species of cynegetic importance takes place in ecotone zones (semi-aquatic environments) or is more common there (ungulates, rodents). The management of hunting territories must take account of these facts;
- The boundary zones of natural parks can either improve preservation or constitute disturbance zones. Their role in the maintenance of biological diversity needs to be carefully studied (Schonewald-Cox et al. 1983, Soulé 1983, SCOPE 1986).

CLASSIFICATION OF ECOTONES

Fundamental to developing a theoretical framework leading to increased understanding of ecotones is a useful functional classification. Because the working definition we are using for ecotones is relatively abstract, this classification should be designed to promote theory development. There are many possible criteria which could be employed in the classification of ecotones. We shall focus on two approaches. One distinguishes between events that cause or maintain ecotones. The other approach involves the structure and function of ecotones themselves. Our primary purpose here is to challenge present thinking on ecotones and to stimulate discussion.

Events that create or maintain ecotones may be caused by humans or by natural processes. Furthermore, these events may be internal to one ecotone or external to it. Figure 4 depicts four cases of controls for origination and maintenance of ecotones, and gives an example of each of these cases. For instance, the ecotone between a beaver (*Castor canadensis*) pond and its adjacent forest is determined by the interaction of a variety of natural variables, including nature of resources, predation pressure, and geomorphology of the region (Johnston and Naiman 1987). On the other hand, strips of riparian forest may be retained in an agricultural landscape by local residents. Such ecotones are maintained by human controls, external to the ecotone.

Distinguishing between external and internal causal mechanisms is important for the study and management of ecotones. Ecotones may be categorized according to the response of the biological variable of interest (response variable) to some controlling variable. An ecotone appears as a relatively large change of the response variable over a small interval and may be generated by external or internal factors (Figure 5).

		Maintenance	
		Human	Natural
Origin	Human	Transition zones around tropical ponds built and maintained for food production	Wetland transitions zones that form around reservoirs with controlled water level regimes
	Natural	Strips of riparian forest retained in an agricultural landscape	Transition zones around beaver ponds

Figure 4. **A scheme for classifying ecotones that distinguishes between ecotones caused and maintained by human versus natural mechanisms. Examples are given in each cell.**

If the response variable is proportionally related to the control variable (Figure 5, Type 1), an ecotone can occur only if there is some discontinuity in the control variable (e.g., a steepening of the soil moisture gradient due to a catena effect). In this case, the ecotone is maintained by external control.

Alternatively, the biological variable may exhibit a discontinuous response to the gradient of the control variable (Figure 5, Type 2). Here an ecotone can occur even along a smooth control gradient. The ecotone is generated by factors internal to the ecological system (e.g. successional processes following natural tree death).

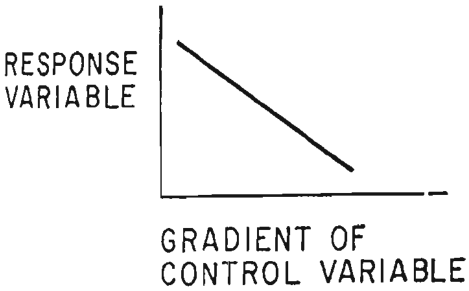
Internal factors may also produce a hysteretic relationship between the response and control variables (Figure 5, Type 3). Once again, an ecotone can occur along a smoothly changing control variable. The location of the ecotone is history dependent. For example, the position of the taiga/tundra boundary occurred at a lower temperature isocline as global temperatures dropped during the Pleistocene than when temperatures increased during the Holocene. This hysteretic effect was due to the presence of permafrost when temperatures began to rise. In another example, a "zone of hysteresis" exists in communities of the Caucasus forest when there are analogous feedback structures not only due to changes in time, but also in space, on one or on both sides of the limits for a natural landscape (Armand 1985).

The distinction between external and internal controlling variables have important implications for management. For instance, one important example of an ecotone is the boundary between agricultural land and natural ecosystems. Generally these ecotones can be thought of as a Type 1 response (Figure 5) in which human management activities create the discontinuity in the control variable. When these human activities are relaxed or ceased, succession processes would tend to restore the system to a state in which the ecotone would disappear. Type 2 or Type 3 ecotones would persist without management. In Type 3 systems, if management displaced an ecotone to a new position, the ecotone would remain in its new position even if the management were ceased. Thus, the responses of the three categories of ecotones to management are different.

The differences between ecotones created or maintained by internal versus external mechanisms or by human versus natural phenomena are partially due to differences in scale between these phenomena. Clearly, events that are relatively frequent, large in area, or intense will maintain greater contrasts between an ecotone and adjacent ecological systems than will events that are of lesser scale. Thus, ecotones can be classified more precisely by quantifying the temporal scales, spatial scales and the magnitudes of the events that cause or maintain them. Figure 6 lists some variables useful in this regard.

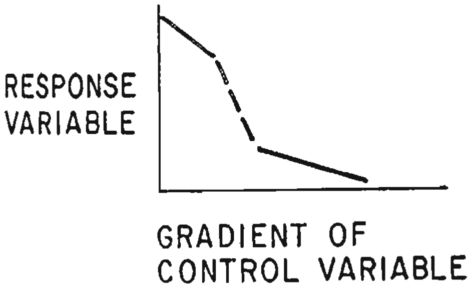
ECOTONE FEATURES

Type 1



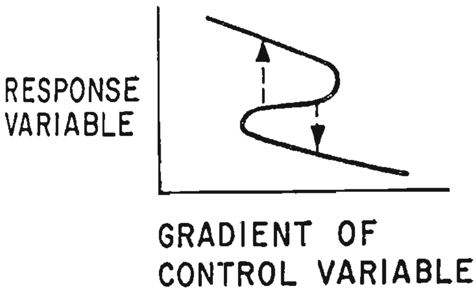
Ecotone can occur only if there is some discontinuity in the control variable (for example, steepening of soil moisture gradient). Ecotone is maintained by external control. There is no ecotone without this discontinuity.

Type 2



Ecotone can occur even along smoothly changing control variable. Factors internal to the ecological system generate ecotone (for example, successional processes following natural tree death).

Type 3



Ecotone can occur even along smoothly changing control variable. Location of the ecotone is history dependent. Factors internal to ecological system generate ecotone (see text for example).

Figure 5. **Theoretical 3-level functional categorization of ecotones.**

TEMPORAL SCALES

Frequency - occurrences per unit time.
Duration (Longevity) - length of time over which an event has been repeated.

SPATIAL SCALE

Size - proportion of ecotonal area or volume influenced by the event.
Shape - the shape of the ecotonal region influenced by the event.

MAGNITUDE

Intensity - the strength or magnitude of the event.
Severity - the strength or magnitude of response by the biota to the event.

Figure 6. **Some variables that are useful for quantifying the scale of the events that create or maintain ecotones.**

Consideration of scale is particularly relevant to differentiating between some human impacts and natural events for three reasons. First, humans sometimes alter the scale of natural agents that create or maintain ecotones (Urban et al. 1987). Fire suppression programmes, for example, often result in less frequent but more intense fires than under natural conditions. Second, humans have introduced new types of phenomena that are functionally similar to natural events but are of greater scale. Timber harvest typically occurs at an intensity, frequency, and spatial scale that creates more numerous and more abrupt ecotones than windthrow. Third, humans have introduced phenomena that have no natural counterparts (e.g. urbanization). Much of the biota is poorly adapted to these novel phenomena. Consequently, the biota often respond more dramatically to these regimes than to those of greater longevity.

Development of theory on ecotones can also be enhanced by classification schemes based on the structure and functioning of ecotones. Such an approach has been implemented in the classification of ecosystems with some success (Sims, Singh and Lauenroth 1978). Some of the variables that may be useful are listed below.

Structural Variables

Size - the area or volume of the ecotone relative to the size of the adjacent ecological systems and the spatial scales of flows between ecological systems.

Shape - e.g., linear or circular. Landscape ecologists are increasingly exploring the relationships between patch shape, patch volume, and rates of flows across and along patches (Forman and Godron 1986). This seems particularly applicable to ecotones.

Biotic Structure - e.g. distribution of biomass or density of dominant organisms.

Structural Contrast - the extent of difference between the ecotone and the adjacent ecological systems in biotic structure.

Functional Variables

Stability - degree to which the ecotones resist change under stress.

Resiliency - rates at which ecotones return to an initial condition following stress.

Energetics - e.g. productivity of dominant organisms, and flow of matter and energy between ecotone and its surroundings.

Functional Contrast - the extent of difference in the functional variables above between ecotones and adjacent ecological systems.

It appears that the classification approaches described above may be useful for understanding and managing ecotones. Clearly, refinements of these schemes will be needed for resolving specific questions about ecotones. However, this classification scheme may prove helpful in stimulating discussion leading to development of general theories about the ecotone concept.

MONITORING OF ECOTONES FOR ASSESSING GLOBAL CHANGES

The extent to which ecotones may be affected by global changes (e.g. increases in atmospheric CO_2) is at the present time not predictable. This situation can be improved by finding a means of relating biotic processes that we understand (from ground measurements) to larger-scale patterns that we can measure rather easily through spatial remote sensing techniques. Only recently have scientists attempted to explain such relationships between pattern and process.

Remote sensing supplies a way of objectively measuring lines of transition (or boundaries) at several spatial resolutions and of tracking vegetation changes on a quantitative basis. At the present time, satellite remote sensing operating in the visible and near infrared spectral domain, allows monitoring terrestrial features with spatial resolutions ranging from 10^{-2} ha (SPOT) to 10^{2} ha (NOAA/AVHRR). Effective temporal rates of data availability depend on cloud coverage ; typically, cloud-free data may be obtained on a weekly basis (NOAA/AVHRR) or a seasonal basis (LANDSAT, SPOT).

The observation data sets are generally different for the ground-based approach which considers numerous vegetation and environmental variables, and the remote sensing approach which provides only a limited number of measurements (reflected radiances at specific wavelengths). However ecotones may be defined in both cases by the same rigid criteria : steep gradients or break points in the measurements. Furthermore, it seems likely that both approaches can be successfully linked on one or more scales, via common state variables. Leaf area index may prove a useful linking variable, because the index (or a surrogate) can be estimated using either on-site measurements or remote imagery.

Detection of changes may be based on structural or functional criteria:

- spatial structure
  local variance (Woocock and Strahler 1987) may serve well here as an indicator of change. This approach will allow the testing of models of vegetation or landscape spatial pattern which is qualitatively superior to past studies because it will be based on the complete inventory of that pattern (White and MacKenzie 1986).

- functional components
  it is necessary to determine more precisely the relationships between remotely sensed spectral vegetation indices (SVIs) and canopy biophysical parameters. SVIs were shown to be related to intercepted photosynthetically active radiation, but also to the canopy potential transpiration (Sellers 1985); it is therefore potentially possible to use SVIs to estimate the global photosynthetic capacity and the capacity to transpire of a land surface.

A monitoring programme of ecotones based on remote sensing should consider the following requirements :

1. Optimization of spatial resolution

Sharp boundaries are easily detected on satellite imagery; more gradual transition areas require high spatial resolution data in order to characterize spatial aggregation patterns; the use of airbone data, including video imagery obtained from a light air plane (Meisner 1986) could improve the correlation between ground measurements and remotely sensed data ; more generally, the consideration of multiresolution data in a geometric series (i.e. pixel sizes of 6m, 13m, 30m and 80m used by White and MacKenzie 1986) should be recommended, in view of understanding nested spatial patterns at different scales and of relating local studies to regional or global studies.

2. Optimization of spectral resolution

At least two spectral channels (red and near infrared) are needed to detect and quantify healthy green vegetation amount and distribution; more channels could give valuable information on the physiological status of vegetation (i.e. shortwave infrared channels of LANDSAT-TM); the planned development of high resolution imaging spectrometry (airbone experiments in view of operational use with orbital space around 1994-95) could lead to a better link between remote sensing data and ecophysiological data, offering new possibilities for the detection of precursors of ecosystem change (Waring et al. 1986).

3. Operational use of registration procedures

The study of temporal changes lies in the accuracy of the integration of multidate remote sensing data with ancillary data (i.e. digital terrain model) ; from such geocoded data bases, data can be displayed at a variety of scales, revised and reproduced easily, enhancing vegetation changes or trends.

4. Development of explicit spatial models of vegetaion dynamics

Remote sensing data, in spite of their spatial nature, are generally processed on a pixel-by-pixel basis, without taking into account spatial information (texture or structure) ; on the other hand, vegetation dynamics studies often suffer from chronically undersampling, and spatial aspects are treated on a more or less implicit basis. Developing spatial models of vegetation dynamics could be based on mathematical concepts like fractal dimension and self-similarity (Loehle 1983), geostatistical theory (Clark 1979), or catastrophe theory (Saxon and Dudzinski 1984). These concepts may be applied to remote sensing data concerning natural boundaries (i.e. forest/meadow, evergreen/deciduous). More generally, improved monitoring capacities offered by remote sensing should be accompanied by a theoretical effort concerning the formalization of discrete scene models (Strahler et al. 1986), clearly indicating the relationships between spatial and temporal characteristics of ecotones, vegetation with specific spectral signatures, and sensor characteristics.

RESEARCH QUESTIONS

In an effort to stimulate the development of some general theories about ecotones, the working session devoted considerable time to the articulation of testable research questions. The following questions were proposed to generate discussion within the scientific community which will lead to the design of new (or the re-focusing of current) research projects which can begin to address, and ultimately may answer, these questions.

Question 1. To what extent can ecotones be functionally classified so as to facilitate comparisons among different ecotones with respect to origin, structure and ecological processes?

Narrative: The previous section "Classification of Ecotones" suggested that functional classification of ecotones is essential to developing a theoretical framework for an understanding of ecotones. One classification approach emphasized distinguishing between ecotones under internal control versus external control. In this example, ecotones are categorized according to the response of the biological variable (response variable) to some controlling variable. An ecotone appears as a relatively large change of the variable of interest over a small interval of space or time and may be generated by external or internal factors.

Implications: As discussed under "Classification of Ecotones", the features that create and maintain an ecotone have important implications for management. The boundaries between agricultural land and natural ecosystems are a Type 1 response (Figure 5 - "Classification of Ecotones" section) in which human management activities create the discontinuity in the response variable. When these human activities are relaxed or ceased, succession processes would tend to restore the system to a state in which the ecotone would disappear. Type 2 or Type 3 ecotones would persist without management. In Type 3 systems, if management displaced an ecotone to a new position, the ecotone would remain in its new position even if the management were ceased. Thus, the response of the three categories of ecotones to management are different.

Tests: The categorization that has been discussed is intended as an example. Because the behavior of an ecotone in response to manipulations of the controlling variables may be different, it is possible to design experimental protocols that can identify the type of generating case (Figure 5) for a given ecotone. We would like to know what sorts of ecotones occur in different systems and if the types all exist. Further, the development of a classification of ecotones with a comparative, functional basis clearly needs to be developed beyond the example cases that are shown in Figure 5.

Question 2. Do ecotones provide stability for the resource patches they separate and, if so, at what spatial and temporal hierarchical scales do they operate?

Narrative: Ecotones, being created by the resource patches they separate, exist over a variety of spatial and temporal scales. At the same time, the question arises as to what role ecotones may have in influencing the stability (integrity) of adjacent resource patches. Little information exists on the optimal spatial and temporal aspects of ecotones that would influence the stability of adjacent resource patches (Baudry 1984, Forman 1981, Merriam 1984).

For example, pests that de-stabilize agricultural crops often utilize ecotones for parts of their life cycles. There is also the occasional need for artificial ecotones to support the stability of adjacent patches (i.e., windbreaks and riparian forests). Further, the relation between the volume of the ecotone patch and its edge has a postulated influence on genetic and biodiversity of the adjacent patches (Merriam 1986).

Implications: Should ecotones provide stability, the implications are that:

(1) Management of spatial arrangement (size, position, composition) at the appropriate temporal scale would allow maximum utilization of adjacent resource patches in an efficient manner ; and
(2) an understanding of the factors which support that stability would allow system restoration to proceed rapidly with an efficient use of available manpower and resources.

Tests: Test of postulated characteristics will depend upon the nature of the key resources separated by the ecotone and the type of stability which is either desirable or attainable. Nevertheless, use of chronosequences and examination of natural situations existing over contrasting spatial and temporal scales, should provide insights into the stability of various types of ecotones. Coupled with the use of simulation models to help design the field experimentation, the key factors which provide that stability can be examined. This would lead to experimental manipulation in the field. Depending upon the resource, artificial ecotones can be created that differ in size, resource gradients, and longevity. A stress (disturbance) can then be applied and the response measured in the resource patches over differing spatial and temporal scales.

Question 3. What are the key attributes (processes and components) of ecotones which impart resistance and resilience to disturbance of the adjacent resource patches?

Narrative: Implicit within this question is that a good understanding of the pattern and frequency of disturbances exists for each of the structural/functional types of ecotones. The basic question, however, transends the ecotones and is applicable to other ecological systems. The question also implies that ecotones perform a function for the resource patches they separate. There is increasing evidence that ecotones, in some instances, may act as semipermeable membranes between ecological systems to modify the direction, the character and the magnitude of materials and information exchanged by the adjacent ecological systems (Wiens et al. 1985, Johnston and Naiman 1987). The nature of the exchange is determined by the structural and functional properties of the ecotone. The ecotone, as a selective filter, acts to modify disturbances as well as the response of the resource patch to that disturbance. Therefore, within the ecotone it is postulated that there are integral components and processes that differentially act to impart resistance and resilience to a given disturbance. One example can be found in the work of Peterjohn and Correll (1984) on the Rhode River watershed.

Implications:

1. A knowledge of these key attributes would allow efficient management and enhancement of selected attributes to modify the severity of the disturbance.
2. It may also provide a quantification of disturbance in terms of economic and ecological costs.

Tests:

1. Use of experimental ecotonal/resource patch systems subject to various classes of disturbances (i.e., toxic chemicals, wind, fire) of various intensities. Followed by study of the recovery of the resource patch components and processes as well as the ecotone.
2. Use of simulation models to identify key components and processes for empirical experimentation can provide insights into the critical components and processes for resistance/resilience.
3. Multivariate studies of existing data sets. For example, in the Moisie River, Quebec, Canada, Naiman et al. (1987) have shown that total inputs and outputs of carbon can be readily predicted for a given stream order

from the standing stock of coarse wood debris. In this case major metabolic rates can be predicted from a relatively simple measurement of a system component. This was only possible after developing an extensive data base on system structure and processes. A similar approach should be developed for ecotonal dynamics.

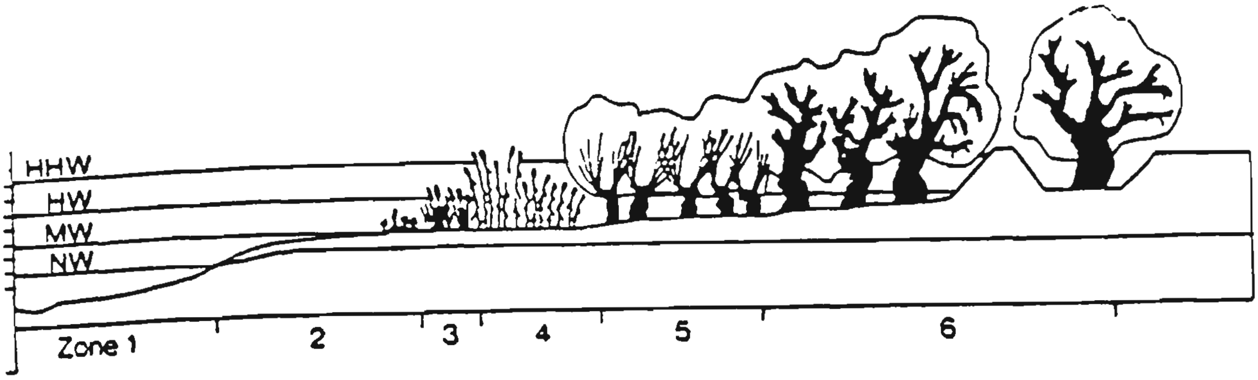
4. Experimental manipulations of existing, reasonably well known sites by:
   a. adding/removing structural complexities
   b. modifying life history characteristics of the plant/soil communities
   c. modifying resource gradients (i.e., nutrients, moisture).

This would provide direct experimental evidence to identify the key ecotonal characteristics for a given disturbance.

Question 4. Is there a predictable pattern to dynamic change in ecotones under natural conditions?

Narrative: Various physical factors can lead to the evolution of plant communities. For example, along a river's edge (Figure 7), erosion, transportation and sedimentation by the river can transform the riparian zone. Biological factors, often related to vegetation dynamics, may interfere with the physical factors. Allogenous-type successions dominate in regularly flooded zones, while autogenous-type successions dominate in zones where the water-table is deepest (Figure 8). In fact, riparian vegetation along rivers is evolving from willow (salix) to oak (Quercus) forest depending on the dynamics of floods and their effects on the processes of erosion and sedimentation. This determines the reversible or irreversible character of the ecotone dynamics. As a whole, regular and frequent variations such as water-table fluctuations ensure the perenniality of plant communities. On the contrary, rare, accidental and high intensity variations provoke evolution towards new equilibria according to the possibilities of penetration by neighbouring species (Pautou and Décamps 1985).

It is also clear from Figures 7 and 8 that the perception of ecotones differ between researchers in relation to the time and spatial scale



Vegetation communities near a river:

1 = Submerged zone

2 = Bank zone

3 = Rush zone

4 = Reed zone

5 = Zone of softwoods

6 = Zone of hardwoods

Levels of inundation :

HHW = very high water

HW = high water

MW = medium water

NW = low water

Figure 7. **Example of approach to an ecotone between aquatic and terrestrial ecological systems. Some researchers see this as a diagram of one ecotone, while others distinguish several ecotones separating different zones : submerged, temporarily submerged, reeds, softwood and hardwood zones (modified from Schäfer 1973).**

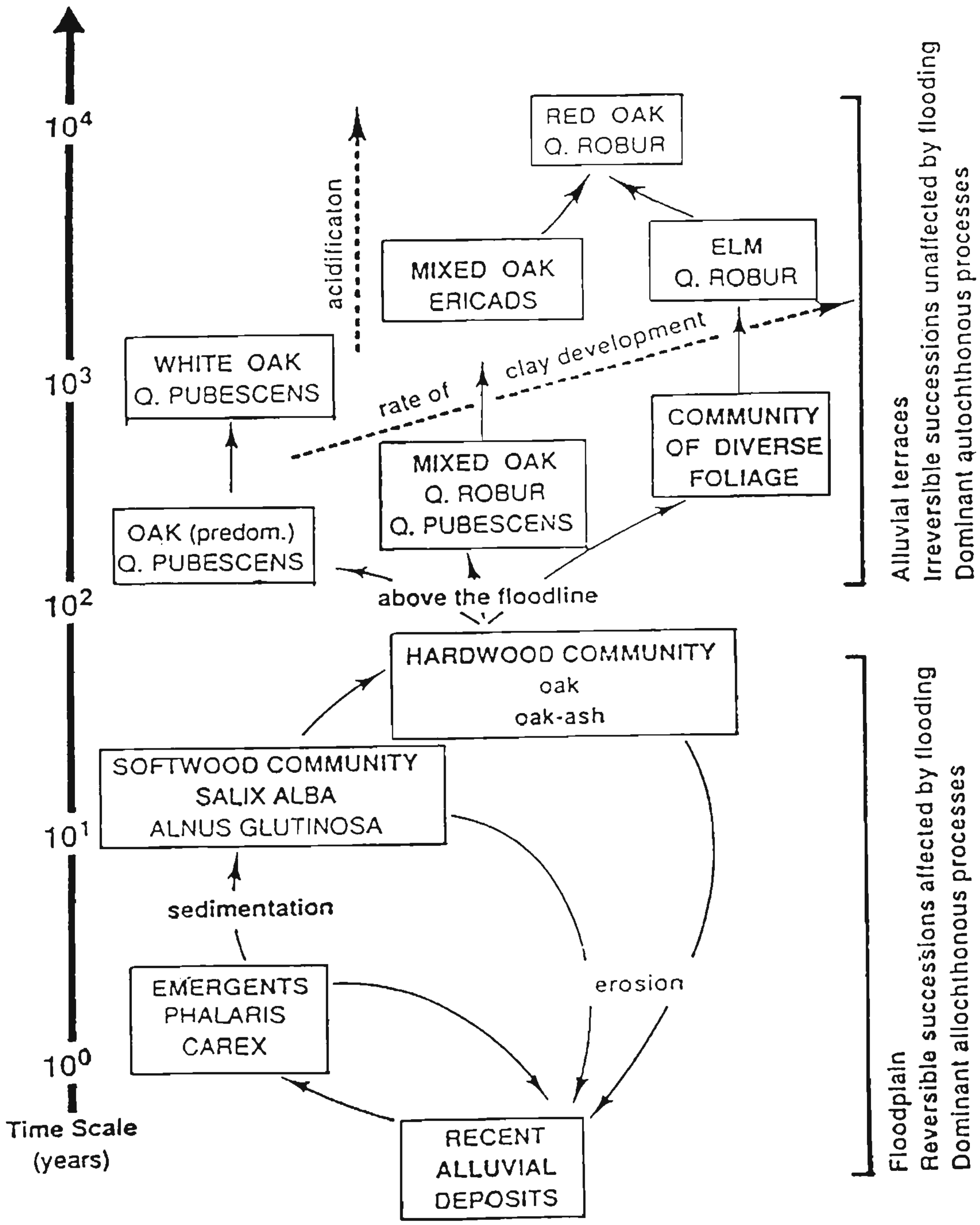


Figure 8. Dynamics of the riparian vegetation along the Garonne River, France, showing the distinction between the reversible and irreversible evolutions in zones influenced or not by floods. Different kinds of successions are predictable in relation to the nature of the substrate (from H. Décamps et al., 1988).

considered. Very different plant communities coexist in the riparian zones of rivers. Some are dominated by a unique monopolistic species while others are highly diversified such as mesohygrophilous prairie communities comprising 40 to 50 species. The spatially diversified ecological conditions with alternating patterns of ridges, depressions and plane surfaces, give rise to mosaics of contrasting substrates, often at different stages of their evolution. Because of their ecological tolerances, certain species are especially liable to invade other communities. Therefore, the riparian zone may be considered functionally as one ecotone, while structurally many different ecotones may be distinguished from river to upland.

Implications: It is important for efficient management of natural systems to know the dynamics of processes in ecotones (Figure 8). Different sequences develop due to the heterogeneity of the area inundated and to changes in the geomorphology of the system (Holland and Burk 1982, 1984). Moreover, the relative importance of autogenic and allogenic processes may vary depending on the plant developmental sequence considered. Temporal variations and the influences of physical factors have to be taken into account, remembering that while trophic stability may be established, physical stability may not be.

Tests :

1. Compare the structure and functioning of chosen ecotones in different hydrological and geomorphological situations along rivers.
2. Consider the changes in the dynamics of processes resulting from a cessation of the interactions between the adjacent ecological systems (for example the impacts of artificial embankment construction on riparian vegetation).

Question 5. How are the characteristics and processes of ecotones sensitive to changes in the global environment ?

Narrative: Although some ecotones from around the world have been studied in various ways (Patou and Décamps 1985, Lauga 1987), there have been no comprehensive attempts to understand the probable sensitivity of ecotones to projected changes in the global environment. Indeed, even general responses are difficult to predict. It is possible, for example, to postulate that because ecotones contain biotic elements at the margins of their distribution and therefore are under stress, ecotones would be sensitive to changes in the global environment and relatively unstable. Alternatively, an equally plausible argument would be to posit that the conditions of ecotones are inherently variable and from an evolutionary basis, contain biotic elements which are relatively immune to changing influences of the global environment. Therefore, the challenge is to discover the general principles that describe the sensitivity to changes in the global environment.

Furthermore, ecotones are postulated to contain greater biomass, resources and biodiversity than the patches they separate; these higher levels may act to impart resistance and resilience to disturbance. Thus, the patches might be the first to show changes. The fact is that we do not know which components would react first.

Implications: Ecotones may represent a number of attributes important both for the understanding and the management of biospheric processes, e.g., support high levels of biological diversity or function as controls for the movement of materials across the landscape. If ecotones are relatively sensitive to changes in the global environment, then it is particularly important to measure the germane attributes of ecotones to obtain early indications of changes in the integrity of the biosphere. Further, such knowledge is mandatory for managing ecotones so as to optimize the ramifications of impacts of changes in the global environment.

Tests: The sensitivity of ecotones to changes in the global environment will involve the following four-step approach:

1. Perform a retrospective evaluation of existing data amenable to analyzing ecotone responses to variables similar to those projected in global change considerations.

   Comments: Weaver and Albertson (1956) describe the shifting of the tallgrass-mixedgrass ecotones in central North America during the drought of the 1930's. Abiotic and biotic responses occurred at different rates; general trends could be predicted from life history characteristics of the dominant plants.

2. Develop a tentative classification of ecotones on the basis of existing data describing responses to these variables, where the attributes in the classification include the putative important characteristics and processes of ecotones.

   Comments: This classification will serve the purpose of organizing subsequent studies, identifying gaps in our knowledge about ecotones, and providing a framework for extrapolating from specific studies of global patterns. Ecosystem types have been classified according to characteristics and processes (e.g., grasslands from Sims, Singh and Lauenroth 1978), so it should be possible to do so for ecotones.

3. Perform an experimental analysis of the actual mechanisms within ecotones that might respond to changing global conditions.

   Comments: Peterjohn and Correll (1984) measured the role of riparian forests in controlling the transfer of nitrogen and phophorus from an adjacent agricultural field to the discharge stream. More nitrogen moved through subsurface pathways and more phosphorus was transfered by surface flow. The riparian forest captured about one-half the nitrogen, some of which was accumulated in the vegetation and some apparently lost via denitrification. Anticipated changes in the global environment might alter the ecotone by affecting important processes, e.g., CO_2 change might change vegetation growth which might affect nitrogen sequestering.

4. Produce synthetic models of ecotone responses to changing global conditions, where the models would range from broad spatial scales of the geographic position of ecotones to finer scales involving specific processes within ecotones, such as successional patterns and nutrient transfer rates.

   Comments: Emanuel et al. (1985) used a specific atmospheric CO_2 climate-change scenario developed by Manabe and Stouffer (1980), and modelled the projected vegetation shifts on a global basis. It should be possible to model ecotones in a similar manner. At finer scales, there are models (Shugart 1984) which could be adapted to accomodate the specific characteristics and processes of ecotones as identified in the preceding three steps.

Question 6. What is the importance of ecotones in maintaining local, regional and global biodiversity?

Narrative: One commonly noted phenomenon in studies of wildlife communities is the "edge-effect" - the tendency for communities to be more dense and often more diverse in ecotonal situations (e.g. see Figure 9). The edge-effect is a generality and probably does not apply to all taxa or to all ecotones. Nevertheless, in cases in which the edge-effect does occur, the biodiversity can be affected by the extent and quality of ecotones (Lovejoy 1979). There are species that are characteristic of ecotones, other species perform activities needed for their survival in ecotones, and the survival/abundance of these species are directly related to the amount of ecotones in an area (Ghiselin 1977). These considerations lead to a need

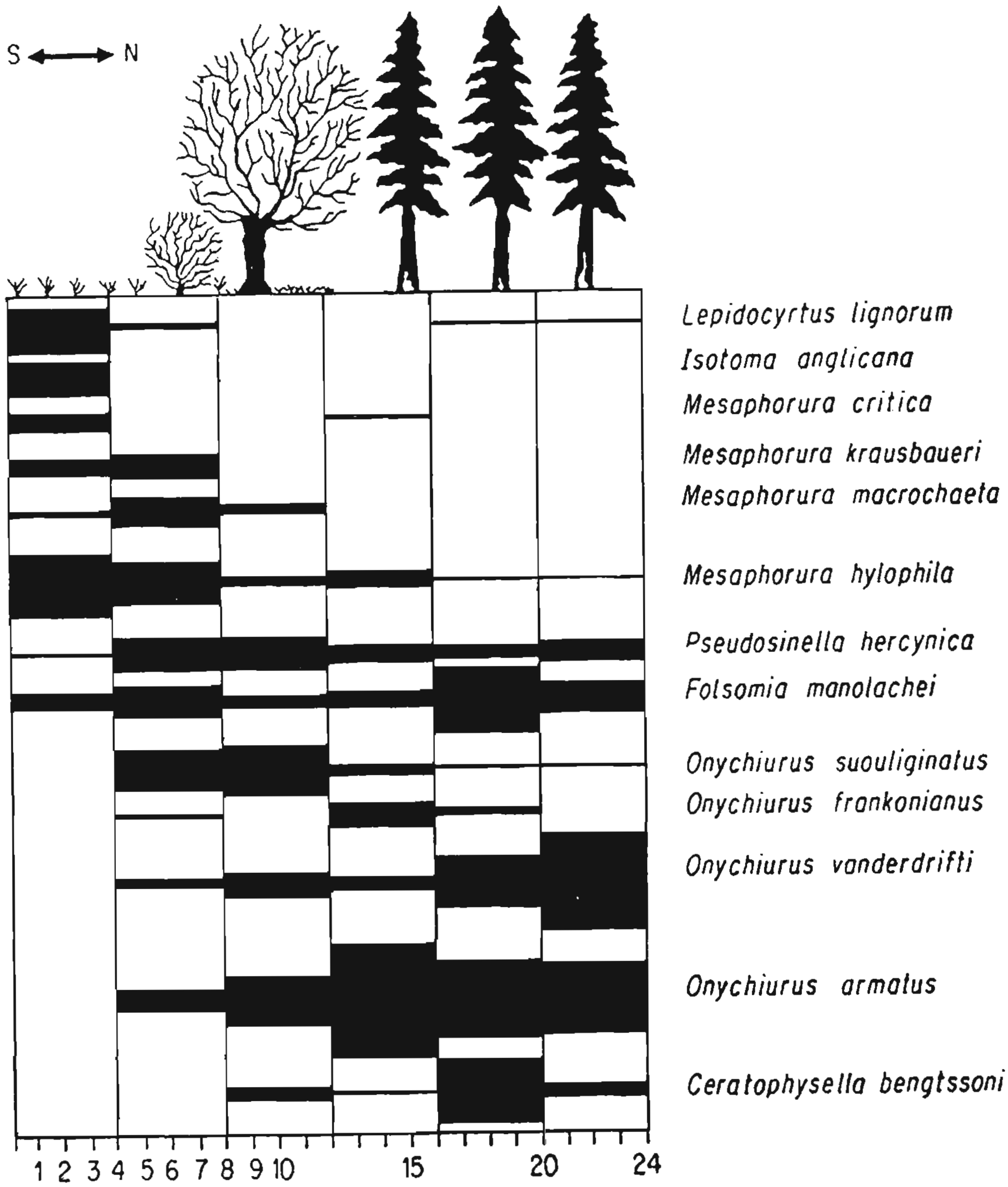


Figure 9. Distribution of some soil inhabiting species of Collembola in a grassland-spruce forest ecotone near Jevany in central Bohemia. Soil samples were taken from 0-10 cm horizon. The thickness of the black lines shows the different densities of certain species in six horizontal zones across the ecotone. Species diversity for the collembolan community was highest on the outer forest margin (H = 2.4), and lowest in the meadow (H = 2.2) (Rusek, unpublished data).

for understanding ecotone/biodiversity relationships in managing landscapes (Goeden 1979). Along with species that are characteristics of ecotones, there are certain animals that require more than one ecological system to survive; examples include: 1) amphibians that breed and lay eggs in water, but live as adults on land; 2) species that feed in one ecological system but rest, nest or hide from predators in another (Diamond 1973); 3) fish that breed in mangroves or marshes and then migrate to the sea as they mature (Odum et al. 1984); 4) birds that migrate from continent to continent using different ecological systems in their breeding area, in their wintering area and also on their way from one to the other (Fitzpatrick 1980, Keast and Morton 1980). These species move through or along ecotones in their movements and the features of ecotones can affect their abundance or survival.

Implications: The potential importance of ecotones for certain species (Beecher 1942) and the importance of large (unfragmented) reserves for others (SCOPE 1986) creates a difficult optimization problem for land managers (Diamond 1978). Fragmented landscapes may have an abundance of ecotones but may not provide suitable habitats for non-ecotone-requiring species (Geis 1974). Consequently, maximizing local diversity by increasing ecotones may lead to a reduction in regional diversity due to a reduction of edge-avoiding species (Gilpin and Diamond 1980, Noss 1983). Studies of biodiversity in fragmented landscape matrices should be coupled with studies of ecotonal species to provide information to resolve this problem.

Tests: Since many game species use ecotones or move through ecotones, there have been tests on some of the procedures that might be used for the management of other ecotonal species. There are also predictive models (mostly for game species) that provide useful examples of model development/model testing protocols (Levin 1977).

Question 7. At what level of human investment have ecotones been maintained and restored in the past? Might that level be expected to continue, diminish or intensify in the future? At what scale are research results most useful for decision-making and management?

Narrative: In many parts of the world, new ecosystems have been created as environmental resources have been put to use, resulting in the development of new and sometimes unique ecotonal boundaries. There has been an attempt to understand and quantify the inherent value of these developments in many countries, but unfortunately the coupling of economic valuation models and ecological concepts has been slow to develop. The intricate interrelationship between ecology and economics has been emphasized emphatically by an expert on international law when he noted, "economic development and environmental protection need not, and must not, be seen as incompatible goals. Indeed, in the long run, they are inseparable" (Springer 1983). In this regard, successful steps in the development of a new, interdisciplinary field of study in ecological economics are encouraging (Thorniley 1986).

The inclusion of increased understanding of ecotones in management practice has in the past included such policies as riparian zone protection (Chiras 1985), hedgerow protection for wildlife conservation (Baudry 1984), and wetlands preservation (Holland and Balco 1985). Recent evidence suggests that the maintenance of some ecotones (e.g. riparian forest in a coastal plain agricultural watershed) may help to minimize the acidification and eutrophication of receiving waters (Peterjohn and Correll 1986). The creation of ecotones seems to be a necessary consequence of some human activities (e.g., conversion of forest systems to agriculture). On the other hand, the reduction of certain natural ecotones (e.g., decrease in contact between rivers and land due to stream channelization) has been a consequence of management activities (Sedell and Froggatt 1984). Recent legislation which recognizes both economic and ecological values of riparian ecotones (Holland and Phelps, 1988) may help to protect some of the remaining gallery forests.

Deliberations of a general scientific advisory panel during the last two years have suggested that the Programme on Man and the Biosphere focus on four themes which cut across many ecosystems (Unesco 1986). These four themes are: 1) ecosystem functioning under different intensities of human impact, 2) management and restoration of human-impacted resources, 3) human investment and resource use, and 4) human response to environmental stress. Human investment as discussed in the panel report includes "investment in social organization, accumulation of knowledge, time and money". This theme requires the integration of knowledge of social perceptions and expectations, with the behaviour of biophysical systems and with the process of investment, disinvestment and reinvestment. Its focus is to examine the linkages and commonalities between the eco in economy and ecology. One project which might be visualized under this theme is the impact of global environmental change (e.g., acid rain or climate change) on regional investment assumptions (Unesco 1986).

Implications: Enlightened management decisions depend on a knowledge of the systems that are affected. The historical inclusion of ecotone-oriented management practice with other land-use policies provides ample precedent for future inclusions of additional information. One of the most abstract concepts to emerge during simultaneous consideration of economic and ecological models has been the idea of "valuation" of natural resources. This holds for both those that have an accepted market exchange and those with non-market values. Since the concept is still abstract, new research efforts are needed to strengthen the ideas, and to make the entire approach more practical.

Tests: To a large degree the inclusion of information on ecotone structure and function in management practice represents the best hope for testing theories about ecotones. Of course, before these theories are likely to be included in management, the necessary scientific testing will be needed to provide convincing arguments for inclusion in management practice. Information on the following topics is needed:

1. Utilization of natural resources in adjacent ecological systems and their ecotones on sustained and non-sustained bases;

2. The inherent market or estimated non-market values of resources being utilized through definition of benefit : cost ratios and by using other models to determine human investment;
3. The types of ecotonal boundaries developed as a direct outcome of the utilization of natural resources;
4. The roles of the specific human societies in maintaining these ecotones, including monetary costs, time investments, and direct returns;
5. New research into analytical approaches, such as environmental resource decision-making models.

RECOMMENDATIONS

The SCOPE/MAB working session provided an opportunity for examining steps for further development of the concept of ecotones. It noted with interest the recent initiative of Unesco/MAB's International Co-ordinating Council in launching a programme on "The role of ecotones in aquatic landscape management and restoration". The group recalled that the fledgling MAB programme on the role of aquatic ecotones is envisaged as a nine-year programme, starting in 1987, with three distinct phases : planning and feasibility (1987-1988), field programme (1989-1993), synthesis and application (1994-1995). The working session welcomed the suggestion that representative scientists from SCOPE participate in the initial planning and feasibility phase of the MAB programme.

This SCOPE/MAB working session resulted in a series of recommendations on possible SCOPE activities on ecotones,

noting that ecotones are potentially important in understanding and managing the biosphere, especially for supporting biotic diversity, maintaining the integrity of energy and material pathways, and providing for primary and secondary productivity,

realizing that some data exist from ecotones around the world but these data have not been organized and synthesized, and recognizing that the topic of ecotones is large and complex, thus requiring a comprehensive and thorough approach involving evaluation of existing data, experimentation, modelling and data interpretation,

recommends that SCOPE establish a scientific advisory committee to direct a three-year data synthesis project on ecotones, and

suggests that this SCOPE project be conducted in close co-operation with the MAB-5 programme on ecotones and with the relevant programme development of IGBP.

In summary, the SCOPE/MAB working session provided an opportunity for exploration of possible avenues for co-operation between MAB and SCOPE with respect to ecotones, as well as potential links with ICSU's International Geosphere-Biosphere Programme. It is envisaged that while SCOPE's three-year data synthesis project on ecotones will result in publication of a state knowledge report on ecotones (see Hansen et al. 1988), the complementary MAB programme on aquatic ecotones will launch a collaborative field research programme in the early 1990's with emphasis on aquatic landscape management and restoration (see Naiman et al. 1988). Thus, the SCOPE/MAB working session recognized the magnitude and complexity of the task at hand, and realized the benefits to all concerned of mutual collaboration in evaluating and clarifying the concept of ecotones.

ACKNOWLEDGEMENTS

This paper was prepared while the compiler was on sabbatical leave with the Man and the Biosphere Programme (MAB), Division of Ecological Sciences, Unesco, Paris. I wish to thank the MAB staff for their hospitality, and for providing me a challenging environment in which to work. I also thank my home institute, the College of New Rochelle in New York, School of Arts and Sciences, for granting me the sabbatical leave. Several people who did not participate in the technical consultation have made valuable comments on various drafts of this report. They are Drs. A. D. Armand, B. von Droste,

J. Gladwell, G. Glaser, C. Gliddon, J. Lepart, B. Lacaze and F. Verhoog. Thanks also go to A. Bugnon, J. Degeorges, J. Draber and S. Rodriguez for typing and re-typing several drafts of this manuscript.

LITERATURE CITED

Acherar, M., J. Lepart and M. Debussche. 1984. La colonisation des friches par le Pin d'Alep (Pinus halepensis Mill.) en Languedoc méditerranéen. Acta Oecol., Oecol. Plant., 5: 179-189.

Armand, A. D. 1985. The change of vegetation near the timber-line. Inter-Nord 17: 59-62.

Barker, G. 1985. Prehistoric farming in Europe. Cambridge University Press. Cambridge, UK.

Bartholomew, B. 1970. Bare zone between California shrub and grassland communities: The role of animals. Science 170: 1210-1212.

Baudry, J. 1984. Effects of landscape structure on biological communities: The case of hedgerow network landscapes. Proc. Int. Sem. IALE "Methodology in landscape ecological research and planning". Roskilde, Denmark, 15-19 October 1984. Vol. 1: 55-65.

Beecher, W. J. 1942. Nesting birds and the vegetation substrate. Chicago Ornithological Society, Chicago, Illinois, USA.

Bellamy, D. J., P. Bridgewater, C. Marshall and W. M. Tickle. 1969. Status of Teesdale rarities. Nature 222: 238-243.

Boaler, S. B. and C. A. H. Hodge. 1962. Vegetation stripes in Somaliland. J. Ecol. 50: 465-474.

Bosson-Lamouille, F., J. C. Lefeuvre, J. Missonier and J. Renard. 1980. Caractéristiques du bocage et conséquences de son aménagement: discussion et conclusions générales. Bulletin technique d'information "Bocage et aménagement rural: quel avenir? Bilan de dix ans de recherches". N° 353-355, pp. 877-898.

Bouchet, R., J. C. Colli and J. Renard. 1980. Avant-propos: un outil de dialogue. Bulletin technique d'information "Bocage et aménagement rural: quel avenir? Bilan de dix ans de recherches". N° 353-355, pp. 615-616.

Burgess, R. L. and D. M. Sharpe, editors. 1981. Forest island dynamics in man-dominated landscapes. Springer Verlag, New York, New York, USA.

Chiras, D. D. 1985. Environmental science: a framework for decision making. The Benjamin/Cummings Publishing Company, Inc. Reading, Massachussets, USA.

Clark, I. 1979. Practical geostatistics. Applied Science Publ. Ltd., Barking, Essex, UK.

Clements, F. E. 1905. Research methods in ecology. University Publishing Co., Lincoln, Nebraska, USA.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Inst. Wash. Publ. N° 242. Arlington, Virginia, USA.

Clements, F. E. 1936. Nature and structure of the climax. J. Ecol., 24: 252-284.

Connell, J. H. and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-44.

Curtis, J. T. 1956. The modification of mid-latitude grasslands and forests by man. Pages 721-736 in W. L. Thomas, editor. Man's role in changing the face of the earth. Univ. of Chicago Press, Chicago, Illinois, USA.

Darby, H. C. 1956. The clearing of the woodland in Europe. Pages 183-216 in W. L. Thomas, editor. Man's role in changing the face of the earth. Univ. of Chicago Press, Chicago, Illinois, USA.

Davis, M. B. 1981. Quaternary history and the stability of forest communities. Pages 132-153 in D. C. West, H. H. Shugart and D. B. Botkin, editors. Forest succession: Concepts and applications. Springer Verlag, New York, New York, USA.

Davis, M. B. 1983. Quaternary history of deciduous forests of eastern North America and Europe. Ann. Missouri Bot. Garden 70: 550-563.

Davis, S. D. and H. A. Mooney. 1985. Comparative water relations of adjacent California shrub and grasslands communities. Oecologia, 66: 522-529.

Debussche, M., J. Lepart and J. Molina. 1985. La dissémination des plantes à fruits charnus par les oiseaux: rôle de la structure de la végétation et impact sur la succession en région méditerranéenne. Oecol. Gener. 6: 65-80.

Décamps, H., M. Fortuné, F. Gazelle and G. Pautou. 1988. Influence des activités humaines sur l évolution de la végétation fluviatile dans la plaine de la Garonne (submitted to Landscape Ecology).

Delcourt, H. R. 1987. The impact of prehistoric agriculture and land occupation on natural vegetation. TREE 2: 39-44.

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science 179: 759-769.

Diamond, J. M. 1978. Critical areas for maintaining viable populations of species. Pages 27-40 in M. Holdgate and M. J. Woodman, editors. Breakdown and restoration of ecosystems. Plenum Press, New York, New York, USA.

Diamond, J. M. and R. M. May. 1981. Island biogeography and the design of natural reserves. Pages 228-252 in R. M. May, editor. Theoretical ecology: Principles and applications. Second Edition. Blackwell Scientific Publications, Oxford, UK.

Drury, W. H. and I. C. T. Nisbet. 1973. Succession. J. Arnold Arboretum 54: 331-368.

Dyer, M. I. and D. A. Crossley. 1986. Summary: "The present as the key to the future". Pages 133-143 in M. I. Dyer and D. A. Crossley, editors. Coupling of ecological studies with remote sensing : potentials at four biosphere reserves in the United States. U.S. Man and the Biosphere Program. Washington, D.C.,USA.

Emanuel, W. R., H. H. Shugart and M. P. Stevenson. 1985. Climate change and the broadscale distribution of terrestrial ecosystem complexes. Climatic Change. Vol. 7: 29-43.

Fitzpatrick, J. W. 1980. The wintering of North American tyrant flycatchers in the neotropics. In J. A. Keast and E. S. Morton, editors. Migrant birds in the neotropics: Ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Forman, R. T. T. 1981. Interaction among landscape elements: A core of landscape ecology. Proc. Int. Congr. Neth. Soc. Landscape Ecol. Veldhoven 1981. Pudoc Wageningen: 35-48.

Forman, R. T. T. and M. Godron. 1986. Landscape Ecology. John Wiley and Sons, New York, New York, USA.

Geis, A. D. 1974. Effects of urbanization and type of urban development on bird populations. Pages 97-105 in J. H. Noyes and D. R. Progulske, editors. A symposium on wildlife in an urbanizing environment. University of Massachussets, Amherst, Massachussets, USA.

Ghiselin, J. 1977. Analyzing ecotones to predict biotic productivity. Environ. Manage. 1: 235:238.

Gilpin, M. E. and J. M. Diamond. 1980. Subdivision of nature reserves and the maintenance of species diversity. Nature 285: 567-568.

Goeden, G. B. 1979. Biogeographic theory as a management tool. Environ. Conserv. 6: 27-32.

Gonzales, G. and H. Casanova. 1987. Etude préliminaire à la caractérisation des forêts riveraines du fleuve Garonne à l'aide de données Landsat MSS et TM. Vingt-sixième assemblée générale du Comité de la recherche spatiale (XXVI COSPAR). 3. Symposium on space observations for regional and global resource assessments: techniques and information requirements. Toulouse, juillet 1986.

Grimm, E. C. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota. New Phytologist 93: 311-350.

Hansen, A. J., F. di Castri and P. G. Risser. 1988. A new SCOPE Project. Ecotones in a changing environment: The theory and management of landscape boundaries. Biology International, Special Issue 17: 137-163.

Hobbs, E. R. 1986. Characterizing the boundary between California annual grassland and Coastal sage scrub with differential profiles. Vegetation 65: 115-126.

Holland, M. M. 1986. Objectives statement for January working session on ecotones, prepared for Unesco/MAB and SCOPE. 1 December 1986.

Holland, M. M. and C. J. Burk. 1982. Relative ages of western Massachussetts oxbow lakes. Northeastern Geology 4(1): 23-32.

Holland, M. M. and C. J. Burk. 1984. The herb strata of three Connecticut River oxbow swamp forests. Rhodora 86(848): 397-415.

Holland, M. M. and J. Balco. 1985. Management of fresh waters: Input of scientific data into policy formulation in the United States. Verh. Internat. Verein. Limnol. 22: 2221-2225.

Holland, M. M. and J. Phelps. 1988. Water resource management: changing perceptions of resource ownership in the United States. Verh. Internat. Verein. Limnol. 23: 2545-2549.

Hopkins, B. 1983. Successional Processes. Pages 605-616 in F. Bourlière, editor. Tropical Savannae. Elsevier, Amsterdam, Netherlands.

Huntley, B. and H. J. B. Birks. 1983. An atlas of past and present pollen maps for Europe 0-13000 years ago. Cambridge University Press, Cambridge, UK.

Jenik, J. 1983. Man-made Biosphere Reserves ? Re-examination of criteria. Pages 214-220 in Conservation, science, and society. Organized by Unesco and UNEP.

Johnson, W. C., P. W. Reily, L. S. Andrews, J. F. McLellan and J. A. Brophy. 1982. Altered hydrology of the Missouri River and its effects on floodplain forest ecosystems. Virginia Water Resources Research Centre, Virginia Polytechnic Institute and State University, Blacksburg Bull. 139. Virginia, USA.

Johnston, C. A. and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landscape Ecology 1: 47-57.

Johnston, D. W. and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37: 50-62.

Keast, A. and E. S. Morton, editors. 1980. Migrant birds in the neotropics: Ecology, behavior, distribution, and conservation. Smithosonian Institution Press, Washington, D.C., USA.

Kullman, L. 1986. Late holocene reproductional patterns of Pinus sylvestris and Picea abies at the forest limit in the central Sweden. Can. J. Bot. 64: 1682-1690.

Lauga, J. 1987. Structures et dynamique d'un corridor fluvial: exemple de la Moyenne Vallée de la Garonne. Rapport Final. Programme Interdisciplinaire de Recherche sur l'Environnement. C.E.R.R. Toulouse, France.

Le Cren, E. D. and R. H. Lowe-McConnell, editors. 1980. The functioning of freshwater ecosystems. IBP N° 22. Cambridge University Press, Cambridge, UK.

Levin, S. A. 1977. Population dynamic models in heterogeneous environments. Annu. Rev. Ecol. Syst. 7: 287-310.

Levin, S.A. 1978. Pattern formation in ecological communities. Pages 433-465 in J. S. Steele, editor. Spatial pattern in plankton communities. Plenum Press, New York, New York, USA.

Levin, S. A. and R. T. Paine. 1974. Disturbance, patch formation and community structure. Proc. Nat. Acad. Sci. (USA) 71: 2744-2747.

Loehle, C. 1983. The fractal dimension and ecology. Speculations in Science and Technology. 6(2): 131-142.

Lovejoy, T. E 1979. Genetic aspects of dwindling populations: A review. Pages 275-279 in S. A. Temple, editor. Endangered birds: Management techniques for preserving threatened species. University of Wisconsin Press, Madison, Wisconsin, USA.

Manabe, S. and R. J. Stouffer. 1980. Sensitivity of a global climate model to an increase of CO_2 concentration in the atmosphere. Journal of Geophysical Research. Vol. 85: 5529-5554.

Margalef, R. 1979. The organization of space. Oikos 33: 152-159.

Mayr, E. 1982. Speciation and macroevolution. Evolution 36: 1119-1132.

McNeilly, T. 1968. Evolution in closely adjacent plant population III. Agrostis tenuis on a small copper mine. Heredity, 23: 99:108.

Meiggs, R. 1982. Trees and timbers in the ancient Mediterranean world. Clarendon Press, Oxford, UK.

Meisner, D. E. 1986. Fundamentals of airbone video remote sensing. Remote Sensing of Environment 19(1): 63-79.

Merriam, G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. Proc. 1 Int. Sem. IALE "Methodology in landscape ecological research and planning". Roskilde, Denmark, October 15-19, 1984, Vol. 1: 5-15.

Merriam, G. 1986. Ecological processes in farmland mosaics. Page 238 in Symposium on Landscape Ecology. IV International Congress of Ecology. Syracuse, New York, USA.

Muller, C. and R. del Moral. 1971. Role of animals in suppression of herbs by shrubs. Science 173: 162-163.

Naiman, R. J. 1986. The role of ecotones in landscape management. Prepared for Unesco/MAB on 22 May 1986.

Naiman, R. J., J. M. Melillo, M. A. Lock, T. E. Ford and S. R. Reice. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic continuum. Ecology Vol. 68: 1139-1156.

Naiman, R. J., M. M. Holland, H. Décamps and P. G. Risser. 1988. A new UNESCO programme: Research and management of land/inland water ecotones. Biology International 17: 107-136.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. BioScience. 33: 700-706.

Odum, E. P. 1971. Fundamentals of ecology, third edition. W.B. Saunders Company. Philadelphia, Pennsylvania, USA.

Odum, W. E., T. J. Smith, J. K. Hoover and C. C. McIvor. 1984. The ecology of tidal freshwater marshes of the United States East Coast : A community profile. U.S. Fish Wildl. Serv. FWS/OBS83/17.

Patten, B. C., S. E. Jorgensen, B. Gopal, J. Kvet, H. Loeffler, Y. Svirezhev and J. Tundisi. 1985. Ecotones: An edge approach to gene pool preservation and management in the biosphere. Prospectus for a new SCOPE programme from the Scientific Advisory Committee for wetlands and shallow continental water bodies.

Pautou, G. and H. Décamps. 1985. Ecological interactions between the alluvial forests and hydrology of the Upper Rhone. Arch. Hydrobiol. 104(1): 13-37.

Payette, S. and L. Filion. 1985. White spruce extension at the tree line and recent climatic changes. Can. J. Forest Research 15: 241-251.

Peterjohn, W. T. and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65: 1466-1475.

Peterjohn, W. T. and D. L. Correll. 1986. The effect of riparian forest on the volume and chemical composition of baseflow in an agricultural watershed. Pages 244-258 in D. L. Correll, editor. Watershed research perspectives. Smithonian Institution Press. Washington, D.C., USA.

Pickett, S. T. A. and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Acad. Press., Inc., New York, New York, USA.

Pinay, G. 1986. Relations sol-nappe dans les bois riverains de la Garonne. Etude de la dénitrification. Ph.D. thesis. C.E.R.R. Toulouse, France. 198 pp.

Quinn, R. D. 1986. Mammalian herbivory and resilience in mediterranean climate ecosystems. Pages 113-128 in B. Dell, A. J. M. Hopkins and B. B. Lamont, editors. Resilience in mediterranean-type ecosystems. D. W. Junk Publishers, The Hague,, Netherlands.

Reiners, W. A. and G. E. Lang. 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. Ecology 60: 403-417.

Risser, P. G., compiler. 1985. Spatial and temporal variability of biospheric and geospheric processes: Research needed to determine interactions with global environmental change. Report of a workshop in St. Peterburg, Florida, October 18-November 1, 1985. Sponsored by SCOPE, INTECOL, and ICSU.

Roth, R. R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57: 773-782.

Rusek, J. 1986. Report from the Czechoslovak National Conference "Ecotones resources of genetical diversity of organisms". Prepared for SCOPE on 3 June 1986.

Saxon, E. C. and M. L. Dudzinski. 1984. Biological survey and reserve design by LANDSAT mapper ecoclines. A catastrophe theory approach. Australian Journal of Ecology 9: 117-123.

Schäfer, W. 1973. Alkrhein Verbund am nördlichen Oberrhein. Courier Forschunginstitut Senckenberg 7: 1-63.

Schonewald-Cox, C., S. M. Chamber, B. MacBryde and L. Thomas. 1983. Genetics and conservation. The Benjamin/Cummings Publishing Company, Inc., London, UK.

SCOPE. 1986. Study on ecotones: Preliminary report to the SCOPE Executive Committee. Nairobi, Kenya. 9-12 May 1986.

Sedell, J. R. and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: The isolation of the Willamette River, Oregon, U.S.A., from its floodplain by shagging and streamside forest removal. Verh. Internt. Verein. Limnol. 22: 1828-1834.

Sellers, P. J. 1985. Canopy reflectance, photosynthesis and transpiration. International Journal of Remote Sensing. 6(8): 1335-1377.

Shugart, H. H. 1984. A theory of forest dynamics: The ecological implications of forest succession models. Springer-Verlag, New York, New York, USA.

Sims, P. L., J. S. Singh and W. K. Lauenroth. 1978. The structure and function of 10 western North America grasslands. I. Abiotic and vegetational characteristics. Journal of Ecology. Vol. 66: 251-285.

Soule, M. E. 1983. Applications of genetics and population biology: The what, where and how of nature reserves. Pages 252-264 _in_ Conservation, science, and society. Organized by Unesco and UNEP.

Springer, A. L. 1983. The international law of pollution: Protecting the global environment in a world of sovereign states. Quorum Books, London, UK.

Strahler, A. H., C. E. Woodcock and J. A. Smith. 1986. On the nature of models in remote sensing. Remote Sensing of Environment 20(2): 121-140.

Strelke, W. K. and J. G. Dickson. 1980. Effect of forest clear-cut edge on breeding birds in East Texas. J. Wilde. Manage 44: 559-567.

Thirgood, J. V. 1981. Man and the mediterranean forest. A history of resource depletion. Academic Press, New York, New York, USA.

Thorniley, D. G. 1986. Report on the Vienna Centre Conference on Economics and Ecology held at the Ronneberga Kursgard, Stockholm, Sweden. European Coordination Centre for Research and Documentation in Social Sciences. Vienna, Austria.

Tranquillini, N. 1983. Frost drought and its ecological significance. Pages 379-400 in O. L. Lange, P. S. Nobel, C. B. Osmond, H. Ziegler, editors. Physiological plant ecology II. Water relations and carbon assimilation. Springer-Verlag, Berlin. 747 pp.

Unesco. 1986. Final Report of the General Scientific Advisory Panel on the Programme on Man and the Biosphere, established in co-operation with ICSU. Banff/Calgary, August 1985, and Paris, April 1986. MAB report series N° 59.

Urban, D. L., R. V. O'Neill and H. H. Shugart. 1987. Landscape ecology: A hierarchical perspective can help scientists understand spatial patterns. BioScience 37(2): 119-127.

van Leeuwen, C. G. 1966. A relation of a theoretical approach to pattern and process in vegetation. Wentia 15: 25-46.

van Leeuwen, C. G. and E. van der Maarel. 1971. Pattern and process in coastal dune vegetation. Acta Bot. Neerl. 20: 191-198.

van der Maarel, E. 1976. On the establishment of plant community boundaries. Ber. Deutsch. Bot. Ges. Bd. 89(5): 415-443.

Vruba, E. S. 1985. Environment and evolution: Alternative causes of the temporal distribution of evolutionary event. Suid. Afrikaause Tydskrif vir Wetenskap 81: 220-236.

Waring, R. H., J. D. Aber, J. M. Melillo and B. Moore III. 1986. Precursors of change in terrestrial ecosystems. BioScience 36: 433-438.

Watt, A. S. 1947. Pattern and process in the plant community. J. Ecol. 35: 1-22.

Weaver, J. E. and F. W. Albertson. 1956. Grasslands of the Great Plains: Their nature and use. Johnsen Publ. Co., Lincoln, Nebraska, USA.

Wegner, J. F. and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. J. Appl. Ecol., 16: 349-358.

White, L. P. 1971. Vegetation stripes on sheet wash surfaces. J. Ecol. 59: 615-622.

White, P. S. and M. D. MacKenzie. 1986. Remote sensing and landscape pattern in Great Smoky Mountains National Park Biosphere Reserve, North Carolina and Tennessee. Pages 52-70 in M. I. Dyer and D. A. Crossley, editors. Coupling of ecological studies with remote sensing: Potentials at four biosphere reserves in the United States. U.S. Man and the Biosphere Program, Washington, D.C., USA.

Whitford, P. B. 1983. Man and the equilibrium between deciduous forest and grassland. Pages 163-172 in W. Holzner, M. J. A. Werger and I. Ikusama, editors. Man's impact on vegetation. D.W. Junk Publishers, The Hague, Netherlands.

Wiens, J. A., C. S. Crawford and J. R. Gosz. 1985. Boundary dynamics: A conceptual framework for studying landscape ecosystems. Oikos 45: 421-427.

Woodcook, C. E. and A. H. Strahler. 1987. The factor of scale in remote sensing. Remote Sensing of Environment 21: 311-332.

ANNEX I

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A NEW UNESCO PROGRAMME: RESEARCH AND MANAGEMENT
OF LAND/INLAND WATER ECOTONES

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Abstract. Ecotones, acting as semipermeable boundaries separating adjacent resource patches, are dynamic components of aquatic and terrestrial landscapes. This article examines some fundamental issues concerning the structure and function of ecotones, addresses the scientific focus of an international research programme specifically examining ecotones occurring at the aquatic-terrestrial interface, and discusses the tentative structure of the research programme. Programme development for this decade-long research effort is presently shared by Unesco's Man and the Biosphere Programme, Unesco's International Hydrological Programme, and the International Institute for Applied Systems Analysis.

PROGRAMME RATIONALE

Aquatic ecosystems are often envisioned as systems where processes are linked by the flow of water and materials (Forel 1892, Vannote et al. 1980). This concept has provided a strong theoretical base for developing a holistic perspective for aquatic ecosystems. This perspective has, in recent years, dealt largely with communities and processes occurring within relatively homogeneous patches, such as the epilimnion or hypolimnion of lakes or within pools and riffles of small streams. Yet within these systems there are transition zones (e.g., gradients or discrete boundaries) which either modify or restrict the flows of water and materials between adjacent resource patches (Wiens et al. 1985, Naiman et al. 1988).

Populations and processes in nature are arranged in discrete patches (Pickett and White 1985), boundaries between these patches are readily detected on various spatial and temporal scales (Forman and Godron 1986, Wiens et al. 1985, Frissell et al. 1986), and human activities are increasingly dividing the landscape into patches with clearly defined boundaries (Hansen et al., this issue). It is difficult to apply transition or continuum concepts (Vannote et al. 1980) to natural systems where sharply defined zones exist or to systems experiencing sustained anthropogenic alterations.

We suggest, therefore, it may be informative to view aquatic systems as a collection of resource patches separated by ecotones or boundaries (Naiman et al. 1988). This concept has been implicitly expressed by others concerned with biotic zonation (Huet 1949 and 1954, Illies 1961, Illies and Botosaneanu 1963, Hawkins 1985) and by those attempting to understand the diversity of communities and interactions encountered on some of the world's large rivers (Rzoska 1978). The ecotone concept also addresses lateral linkages (e.g., channel-riparian forest exchanges) within the aquatic system rather than only longitudinal linkages (e.g., upstream-downstream, Ward and Stanford 1988) or vertical linkages (e.g., epilimnion-hypolimnion, Wetzel 1975). This concept also overcomes some of the immediate difficulties raised by the river continuum concept of quantifying upstream-downstream linkages over long distances (Vannote et al. 1980, Naiman et al. 1988). Viewing aquatic systems as a collection of resource patches separated by ecotones allows the relative importance of upstream-downstream linkages, lateral linkages, and vertical linkages to be examined, and provides a conceptual framework for understanding of factors regulating the exchange of energy and materials between identifiable resource patches (Forman 1981).

The notion of ecotones was used by Clements (1905) to denote the junction zone between two communities, where processes of exchange or competition between neighbouring patches might be readily observed. The term "ecotone" has also been used to refer to interfaces, edges, transition zones, or boundaries between adjacent ecosystems. Based upon operational concerns the MAB Programme has decided to accept the working definition of an ecotone adopted by the MAB/SCOPE Technical Consultation (Holland, this issue).

An increasing number of scientists now believe that a study of ecotones will be of theoretical and practical value (Risser 1985, Wiens et al. 1985, Holland, this issue, Naiman et al. 1988, Décamps et al. 1988). It is assumed that ecotones harbour rich assemblages of flora and fauna, and that they serve as controls for the movement of water and materials throughout the landscape. The potential role of ecotones in prudently managing the biosphere is receiving renewed interest and support because of this. Unesco's Man and the Biosphere (MAB) Programme, Project Area 5, which addresses ecological processes in various freshwater and coastal aquatic ecosystems, is developing a research programme on ecotones being undertaken between 1988 and 1996.

This paper outlines the need for a programme of collaborative research into the role of the land/inland-water ecotones. We suggest the goal of such a programme should be :

> to determine the management options for the conservation and restoration of land/inland-water ecotones through increased understanding of ecological processes.

Special emphasis is being given to ecotones occurring at the terrestrial/aquatic interface because of their importance in regulating the flow of water and materials across the landscape. Such ecotones might include riparian forests, wetlands, littoral lake zones, oxbow lakes, estuaries and areas where groundwater-surface water exchanges are substantial. Programme development is being shared by Unesco's International Hydrological Programme (IHP), MAB, and the International Institute of Applies Systems Analysis (IIASA) because of their common interests and concerns with the aquatic/terrestrial interface.

Considering the key role of land/inland water ecotones, we suggest the specific objectives of the Programme should be :

- To identify the most significant gaps in our present knowledge and understanding;
- To develop a predictive capability for understanding the role of ecological processes within boundaries (ecotones) in determining landscape patterns;
- To develop rational management plans for conservation of ecotones and for use in addressing detrimental environmental practices;
- To develop a collaborative research programme on the theme of recovery and restoration of degraded ecotones occurring at the aquatic/terrestrial interface.

SCIENTIFIC FOCUS

The MAB/IHP Programme is attempting to provide a synthetic viewpoint, emphasizing fundamental structures and processes, having equal applicability to streams, rivers, lakes, wetlands, estuaries, and subsurface aquatic ecosystems. This programme is considering, therefore, several topics relating to ecotones including :

- The inherent characteristics of ecotones that provide for their understanding and classification;
- The responsiveness of ecotones to various forms of disturbance or global environmental change;

- The development of descriptive and predictive models associated with specific structural and functional properties;
- The continued development of theoretical and conceptual models to advance the creative aspects of the field program;
- The practical aspects of the results for better management of natural resources;
- The social and economic benefits of a practical management program.

Rationale for Topics

Characteristics and Classification.

There are several reasons why it would be useful to have a classification of ecotones: organization of information; realistic comparison and extrapolation of information; and development of coherent management approaches. Traditionally ecosystems have been classified by dominant or conspicuous characteristics, physical or climatical characteristics, mode of origin, and human use attributes (Frissell et al. 1986, Turner 1987). Thus, it might be appropriate to classify ecotones according to one or more of these conventional characteristics, or, perhaps, the transitional nature of ecotones will lead to a different classification system, possibly based on functional characteristics.

A combination of structural and functional characteristics could be used (Frissell et al. 1986, Hobbs 1986, McCoy et al. 1986), yet neither set of characteristics is well known for the heterogeneous domain of an ecotone. For example, functional processes, such as production and decomposition rates, have been studied in more or less uniform ecosystems, but transitional zones such as ecotones have received far less attention (Peterjohn and Correll 1984, Ford and Naiman 1988). Fascinating questions arise as to whether, for example, nutrient cycling and energy flow rates are faster or more variable in ecotones than within the interior of a resource patch. Similar questions arise concerning population and community characteristics such as rates of speciation and succession.

By definition, ecotones are transition zones and, as a result, the concept of driving variables assumes a position of paramount importance. Indeed, there are driving variables for the internal processes and other driving variables for the external ones which define the ecotonal characteristics. Presumably hydrographic variables are the most important ones in land-water ecotones (Shugart 1984, Ford and Naiman 1988). However, the strength of these controlling variables may decrease near the extremity of the ecotones and other driving variables may become more important. Characterization of the relative and changing importance of these driving variables will be necessary to form a basis for explaining ecological processes in ecotones.

Responsiveness to Environmental Change.

Among the interesting aspects of ecotones are ways in which these transitional zones respond to changes in controlling variables. The questions involve not only the source of the changes in controlling variables, e.g. natural or human, but whether the changes are caused by local, regional or global factors. Furthermore, the responses may involve only certain components of ecotones and in each case, the response time may be rapid, slow, delayed, linear or non-linear. The response of each component depends on the prior condition of the ecotone with the result that the behaviour of single or multiple components may be cumulative, be increased synergistically, or be attenuated. On the Garonne River in France and in streams in northern Minnesota, U.S.A., we have found that ecotones respond in complex ways to apparently simple controlling variables (Naiman et al. 1988). Both systems exhibit multisuccessional pathways for plant community dynamics and nutrient cycling depending upon when and how the ecotone is disturbed during the ontogeny of patch development. On the Garonne River the community eventually becomes dominated by red oak (Quercus robur) after about 1000 years, but in Minnesota the plant community may become either emergent marsh, forested bog, or an active stream channel depending upon topography and the intensity of activities by beaver (Castor canadensis). Fundamental comparisons of ecotone responses, such as these, will evaluate relative differences among ecotone types and their adjacent or connected ecosystems.

Related to the response characteristics of ecotones is their usefulness in detecting or monitoring global change. It has been postulated that ecotones may be the first to adjust to human influences on the environment and, therefore, may be important in examining the processes involved in global change (Holland, this issue, Naiman et al. 1988). Many of these adjustments occur over realistic temporal and spatial scales for study, and thus would be excellent candidates for the proposed International Geosphere-Biosphere Observatory Programme (Dyer et al. 1988). Management of boundaries, with a view towards maintaining the continued health and well-being of the landscape is, as yet, in an early stage of development but promises to yield substantial practical information.

Descriptive and Predictive Models.

The complexity of ecotones makes them particularly amenable to systems analysis and the application of models (Naiman et al. 1988). These explanatory tools have proven useful in describing a number of fundamental properties, such as energy flow, nutrient cycling and species population dynamics (Shugart 1984). Less frequently, models have been used to describe population migration and dispersion patterns as a function of habitat structure or resource availability (Jenkins 1980). Because of the heterogeneous nature of ecotones as edges or boundaries, new challenges will be faced in constructing these descriptive models (McCoy et al. 1986, Johnston and Naiman 1987). Currently, it is not possible to decide the degree to which the behaviour of ecotones can be predicted; however, the degree to which this is feasible will undoubtedly be enhanced by the development and application of models. In the long term, these models will be used to assist in the management of ecotones, particularly by identifying parameters to be monitored and for clarifying the probable consequences of alternative management strategies.

Theoretical and Conceptual.

Many existing theories about the behaviour of ecological systems have been derived from relatively homogeneous ecosystéms. Ecotones, with their heterogeneous characteristics, offer new opportunities to test conceptual ideas, not just in ecotones themselves but in the relationships between ecotones and their adjacent ecological systems. Thus, possibilities exist for using ecotones as a basis for evaluating theories, such as stability-resilience, patch-interactions, flowpath and hierarchy (Forman and Godron 1981, 1986).

Management : Conservation, Restoration and Creation.

Landscapes consist of a heterogeneous mosaic of resource patches, among which are ecotones. As a result, ecotones are an integral part of the landscape and may play a large role in the control of abiotic and biotic fluxes. For example, riparian transitional forests along streams capture significant amounts of nutrients and sediments (Peterjohn and Correll 1984, 1986, Pinay 1986). The size and configuration, and successional stage of these forest ecotones are important attributes which determine the ways in which nutrients and sediments move across the landscape (Fustec et al. 1988). In addition, these same characteristics also influence the movement and population structure of biological groups, such as birds and small mammals (Décamps et al. 1987, Johnston and Naiman 1987, 1988). Management must consider the ways in which these transitional systems interact with biotic and abiotic fluxes in a rapidly changing global environment.

Ecotones around the world are being created and destroyed by both natural and human processes (Lovėjoy et al. 1986, Franklin and Forman 1987). Historical changes induced by humans have strongly influenced the dynamics of ecotones in fluvial landscapes in rural as well as in urban environments (Holland and Burk 1982, Sedell and Froggatt 1984, Fortuné 1988). Since ecotones are so important but have been subjected to so many anthropogenic impacts, it is imperative to understand how ecotones should be managed, conserved, restored and, if necessary, created. Appropriate management approaches will depend upon an understanding of the behaviour of ecotones and the socio-economic constraints of human systems.

Socio-economic Implications.

Ecotones perform a number of services for the human and non-human components of the biosphere. Therefore, there is a particular urgency in the need to quantify the multitude of values of ecotones and, if possible, to describe these values in monetary terms. These evaluations must include both the short-term and long-term socio-economic implications as well as the dynamics of how these values are expected to change as ecotones sustain spatial and temporal cumulative impacts.

QUESTIONS AND HYPOTHESES

The approach used to develop a scientific focus revolves around a series of questions and hypotheses relating directly to the empirical testing of ecotonal characteristics. In May, 1988, these characteristics, questions, and hypotheses will be explored during an international symposium on terrestrial-aquatic ecotones, in Sopron, Hungary. The format of the symposium is outlined in the following pages. The results of this symposium will be used to develop an international cooperative research programme extending to 1996. These questions and hypotheses are not comprehensive and are only used to illustrate the array of stimulating problems facing those concerned with dynamic boundaries. Consider the following:

Question 1. What is the importance of ecotones in maintaining local, regional and global biodiversity?

One commonly noted phenomenon in studies of wildlife communities is the edge effect: the tendency for communities to be more dense and often more diverse in transition zones between communities. The edge-effect is a generality and probably does not apply to all taxa or to all ecotones.

Nevertheless, in cases in which the edge-effect does occur, the biodiversity can be affected by the extent and quality of ecotones (Lovejoy 1979). There are species that are characteristic of ecotones, other species perform activities needed for their survival in ecotones, and the survival/abundance of these species are directly related to the amount of ecotones in an area (Ghiselin 1977). These considerations lead to a need for understanding ecotone/biodiversity relationships in managing landscapes (Goeden 1979). Along with species that are characteristic of ecotones, there are certain animals that require more than one ecological system to survive such as: insects developing as aquatic larvae but living as adults on land; species that feed in one ecological system but rest, nest or hide from predators in another (Diamond 1973); fish that breed in mangroves or marshes and then migrate to the sea as they mature (Odum et al. 1984); or birds that migrate from continent to continent using different ecological systems in their breeding area, in their wintering area and also on their way from one to the other (Fitzpatrick 1980; Keast and Morton 1980). These species move through or along ecotones in their migrations and the features of ecotones can affect their abundance or survival.

Hypotheses:

H_1: Ecotones are characterized by higher biological diversity than adjacent patches.

H_2: The frequency of ecotones across a landscape directly affects biodiversity in a predictable way (Fig. 1).

Question 2. Which functions do ecotones have, and to what degree do ecotones exert filter effects?

There is considerable evidence that ecotones, such as riparian forest strips, act as filters in the flowpaths of nutrients across the landscape. Peterjohn and Correll (1984) showed, for example, that a riparian forest in a Maryland, U.S.A., agricultural watershed retained 89 % of the nitrogen it received compared to 8 % for adjacent cropland, thus substantially reducing

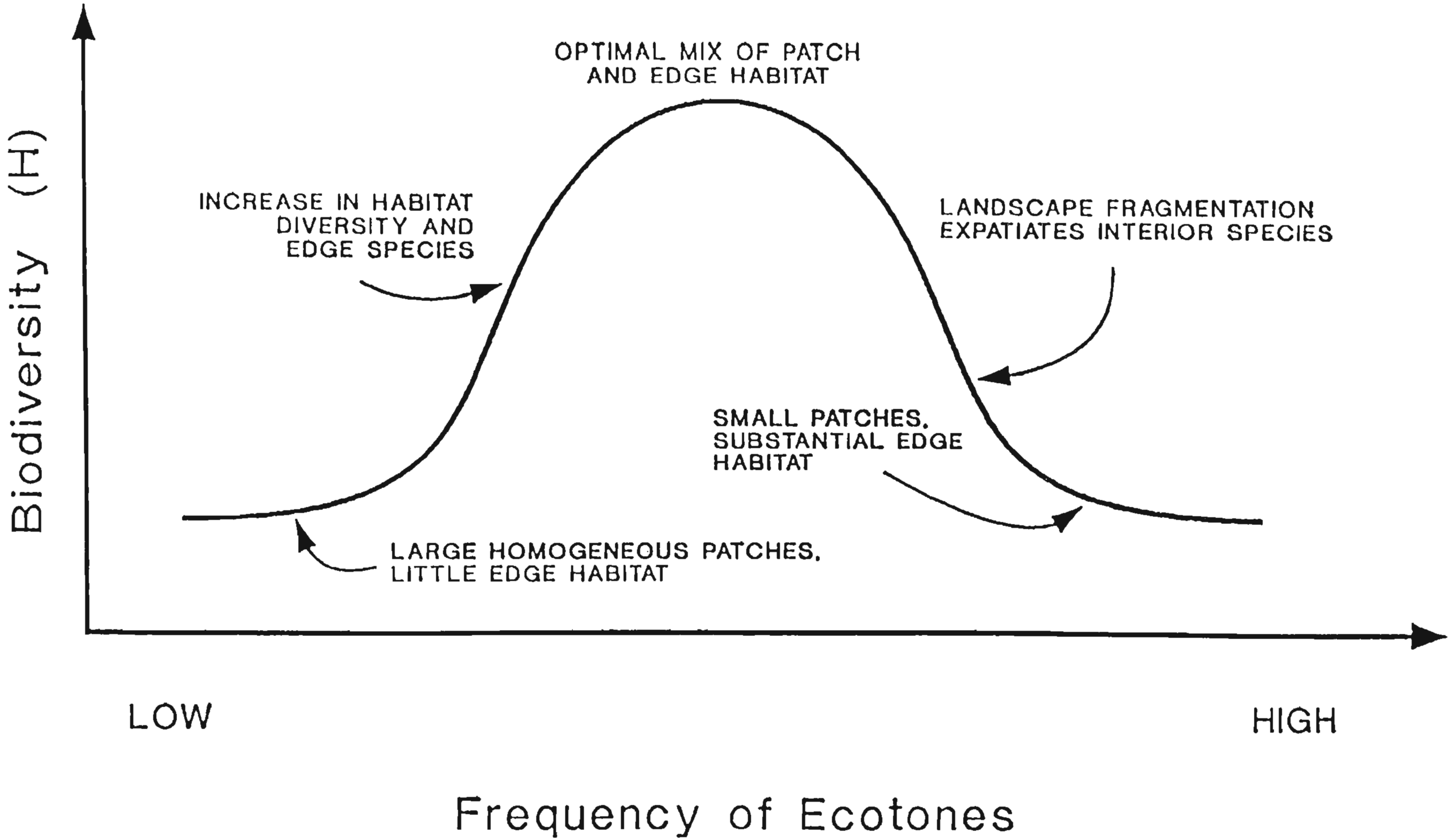

Figure 1. We suggest that the frequency of ecotones can affect biodiversity in a predictable manner by affecting the ratio between patch size and edge length.

nitrogen loss into the receiving stream. In general, significant amounts of N, P, organic matter and sediment are retained by ecotonal riparian forests (Correll 1986).

An important question involves the prediction of the filtering efficacy. In the Peterjohn and Correll study, subsurface pathways were more important for nitrogen while phosphorus was predominately transported while attached to soil particles as overland flow. Also, the nitrogen lost from the system in the riparian forest was greater than what could be accounted for by tree growth. From a practical point of view, Pinay and Décamps (1988) showed that about 30 metres of groundwater flow under a riparian wood in the Garonne Valley was enough to remove nitrate from the groundwater. Thus, the "filtering" process involves several components, e.g., subsurface flow, overland flow, denitrification, and nutrient immobilization by physical-chemical or biological means. Therefore, the challenge is to develop single models to predict the power of these ecotonal filters, probably as a function of the rate of subsurface water flow, uptake by vegetation growth, and denitrification from the soil. Similarly, the annual productivity of the riparian forest might need to be modified to capture the seasonal nature of plant growth. That is, if a forest contains a set of phenological stages with growth through most of the year this term would be greater than forests with growth during only part of the year. Finally, the soil organic matter term might need to be modified by the percent of time the soil is at or near saturation, by the C/N ratio of the incoming leaf litter, and the characteristics of subsurface water flows.

This relatively simple model can then be tested in various riparian ecotones throughout the world. This model can be used in management decisions and in the calculation of socio-economic benefits of ecotones to the degree that it is successful in predicting nitrogen uptake. On the other hand, if the model is unsuccessful in predicting nitrogen uptake, we then learn about the veracity of the model and the multiplicity of nutrient processes in ecotones. Obviously this idea is particularly amenable to an international effort since it not only involves a relatively straightforward structure but demands the coordinated effort of collaborators around the world. In addition, if successful, the model would show that the protection and establishment of riparian forest "buffer strips" should be seriously considered as a management practice on agricultural watersheds. Other recent works support this conclusion (Petersen et al. 1987, Ford and Naiman 1988, Fustec et al. 1988, Pinay and Décamps 1988).

Hypotheses:

H_1: Ecotones strongly influence the adjacent ecosystems and frequently exert an important filter function.

H_2: Management techniques may successfully maintain or enhance the functions of ecotones.

Question 3. Is there any influence of ecotones on the stability of adjacent patches?

Ecotones exist over a variety of spatial and temporal scales. Ecotones may play a role in affecting the stability of resource patches, since they are created by the resource patches they separate. At present, few studies are available on the optimal spatial and temporal aspects of ecotones which might influence the stability of adjacent resource patches (Baudry 1984, Forman 1984, Pringle et al. 1988). Recent studies suggest that the relation between the volume of the resource patch and its ecotone has an important influence on the genetic biodiversity and interactions with the adjacent patches (Merriam 1984, Johnston and Naiman 1987).

Hypotheses:

H_1: An ecotone affects the resistance and resilience of adjacent patches to disturbance by regulating the flow of matter and energy between the patches.

H_2: The stability of the landscape (i.e., patch mosaics) is regulated by the density, size, diversity, and persistence of ecotones between major patches.

H_3: The manner by which an ecotone is formed affects the stability (persistence) of the ecotone and its role in providing stability for the adjacent patches.

Question 4. At what level of human investment have ecotones been maintained and restored in the past? Related questions may include: Might that level be expected to continue, diminish or intensify in the future? At what scale are research results most useful for decision-making and management?

Since ecotones often may be the first to show changes resulting from human influences on the environment, natural resource managers need to consider the role of ecotones in development of wise management plans for natural environments (Holland, this issue). Certainly, human control of the hydrologic regime has affected the structure and development of various inland water/terrestrial ecotones (Hollis et al. 1988). By now, sufficient numbers of case studies have documented the historical role of humans in modification of catchment basins to allow the development of mathematical models useful to decision-makers for future planning and management (Rast and Holland 1988).

A major problem in ecological research lies in the conceptualization and explanation of the interaction between human activities and natural processes. This problem is exacerbated by differences in approach and assumptions between natural-science and social-science research. Here the concepts of "investment" and "use" are chosen to mediate these differences. Human investment is taken to imply all that the resources mean to a particular cultural community. Resource use is taken to cover the other side of the man-environment equation - the complementary physical interaction of people and resources, and the consequent change in the condition of the resources (Unesco 1986).

The Man and the Biosphere Programme focuses on four themes which cut across many ecosystems and are designed to answer these complex questions (Unesco 1986). These four themes are: (1) ecosystem functioning under different intensities of human impact, (2) management and restoration of human-impacted resources, (3) human investment and resource use, and (4) human response to environmental stress. Human investment includes investment in social organization, accumulation of knowledge, time and money. This theme requires the integration of knowledge of social perceptions and expectations, with the behaviour of biophysical systems and with the process in investment, disinvestment and reinvestment. Its focus is to examine the linkages and commonalities between the eco in economy and ecology. One project which might be visualized under this theme is the impact of global environmental change (e.g., acid rain or climate change) on regional investment assumptions (Unesco 1986).

Hypotheses:

H_1: Traditional management techniques have successfully maintained or enhanced the functions of ecotones in the past.

H_2: Descriptive and predictive models can be useful to decision-makers in the identification of parameters to be monitored and for clarification of probable consequences of ecotone management options.

Summary

These questions and hypotheses will be discussed and further elaborated upon at the May 1988 symposium in Sopron, Hungary. Eventually, it is anticipated that they will provide a starting point for the field research phase of the MAB/IHP ecotone programme. This field research phase will be launched on a comparative basis of the various land/water ecotones from different climatic situations in developed and developing countries, and considering natural as well as controlled situations. We expect that a substantive proposal for a comprehensive research programme will have evolved from these questions by the conclusion of the symposium.

PROGRAMME STRUCTURE

The MAB/IHP programme on aquatic/terrestrial interfaces is envisioned as a 10-year project (Table 1) (Fig. 2). Programme development can be broken down into two phases: (1) a short-term synthetic phase and (2) a long-term collaborative research programme.

Short-term Programme

An open international symposium on "Land/Inland Water Ecotones: Strategies for Research and Management" is scheduled for 23-27 May 1988 in Sopron, Hungary. This symposium will be concerned with the interface between research and management and will be convened to meet the following goals :

- to produce a synthesis of scientific information on land/inland water ecotones;
- to examine the implication of present knowledge to management;
- to identify gaps in information and understanding, with respect to both scientific hypotheses and the needs of management;
- to explore directions for future collaborative research and action;
- to develop a research prospectus with testable hypotheses.

The intention of the symposium is to prepare a synthesis based on selected issues and processes, with supporting case studies on research and management experience in particular locations and regions (Table 2). More specifically, the expected outcomes from the May 1988 symposium are (1) twelve initial synthetic papers providing a state-of-the-art evaluation of specific topics relating to Land/Inland Water ecotones, and (2) development of a substantive proposal for a comprehensive research programme. The text for this proposal will be developed by a series of discussion groups, and the proposal will be completed by the end of the symposium. Participants will be expected to apply their expertise to a series of fundamental topics addressing key issues pertaining to ecotones.

Table 1. **Timetable of MAB work effort**

Date	Activity
January 1987	MAB/SCOPE consultation on ecotones, Paris
May 1987	*Ad hoc* committee meets to develop detailed proposal (Toulouse, France)
May 1988	Symposium in Sopron, Hungary
August 1988	Edit materials from workshop in Hungary; commence compiling workshop results for publication in MAB Book Series
November 1988	Distribute report widely and solicit proposals from interested research groups
May 1989	Review and approve proposals
1990	Commence first field projects
1991	First workshop for project participants
1992	3 regional workshops for project participants
1993	Evaluation of projects
1994	Complete field projects/project report
1995-96	Synthesis of reports and development of recommendations for management of ecotones; publication(s) in MAB Book Series

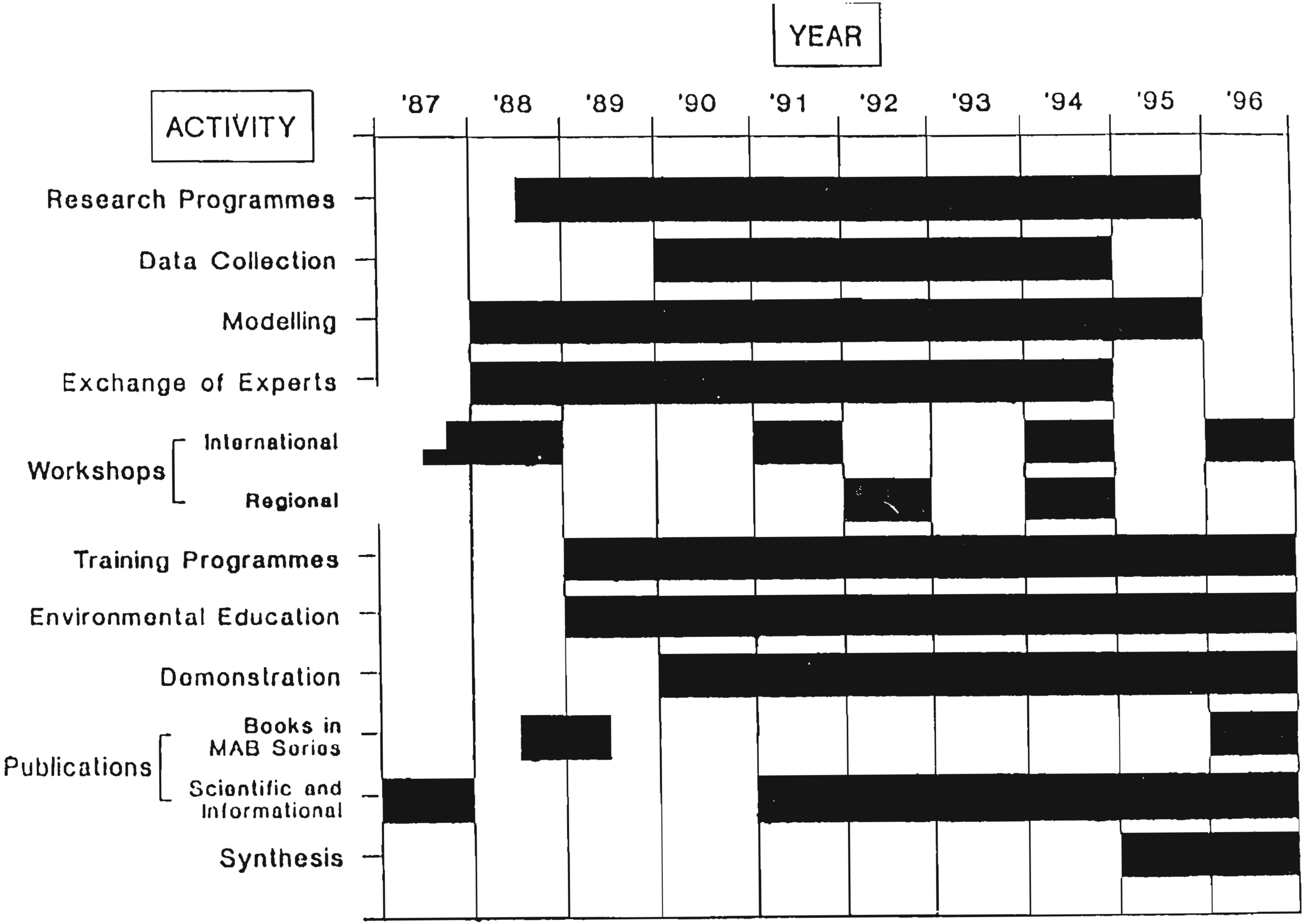

Figure 2. The timetable for general activities associated with the UNESCO Ecotone Programme.

Table 2. **Preliminary outline of plenary lectures for the symposium in Sopron, Hungary**

UNESCO/IIASA

"LAND/INLAND-WATER ECOTONES:
PHASE I - Strategies for Research and Management
a first step for an integrated international programme"

23-27 May 1988 Workshop in Hungary

AREAS OF FOCUS FOR MAY 1988 SYMPOSIUM

I. INTRODUCTION
   A. Preface
      1. Reason for book
      2. Steps
      3. Expected contributions

   B. Historical perspective and importance
      1. Recognition of ecotones and appropriate observational descriptions
      2. Theoretical importance
      3. Practical importance

II. GENERAL PROCESSES
   A. Physical, chemical and biological processes controlling ecotones
      1. Topography, hydrology, geomorphology, climatology
      2. Chemical and biologically important export
      3. Natural and human disturbances (trends)

B. Physical, chemical and biological processes in ecotones
   1. Size, scale, configuration
   2. Energy flow
   3. Biogeochemical cycles
   4. Biological species, population and community dynamics (trends)
   5. Abiotic/biotic interactions

C. Ecotones as tests of theories and models
   1. Patch, hierarchy, diffusion, clusters
   2. Conceptual, dynamic, statistical, stochastic
   3. Stability, resilience, connectivity

D. Ecotones in landscape processes
   1. Control of flows, sediment, nutrient
   2. Contribution to stability
   3. Biodiversity
   4. Human-produced barriers
   5. Size, shape, connectivity

III. STRUCTURE AND FUNCTION

A. Riverine
   1. Physical, chemical, biological structural and functional characteristics
   2. Surface-subsurface systems and hydrological interchanges
   3. Lateral and longitudinal gradients, within and external to ecotone
   4. Community and species dynamics

B. Lake
   1. Physical, chemical, biological structural and functional characteristics
   2. Surface-subsurface systems and hydrological interchanges
   3. Lateral and longitudinal gradients, within and external to ecotone
   4. Community and species dynamics

C. Wetlands

1. Physical, chemical, biological structural and functional characteristics
2. Surface-subsurface systems and hydrological interchanges
3. Lateral and longitudinal gradients, within and external to ecotone
4. Community and species dynamics

D. Groundwater

1. Physical, chemical, biological structural and functional characteristics
2. Surface-subsurface systems and hydrological interchanges
3. Lateral and longitudinal gradients, within and external to ecotone
4. Community and species dynamics

IV. MANAGEMENT

A. Principles and practices : conservation, restoration, creation

1. Connection between research and design criteria
2. Identification of essential attributes
3. Measures of effectiveness, for example, purification

B. Socio-economic values

1. Quantification methodology
2. Incorporation in decision systems
3. Legal/administrative considerations
4. Costs and benefits (monetary and social)

V. SUMMARY

Conclusions and Recommendations

In addition to the invited plenary papers, it is envisaged that six discussion groups will meet throughout the week. Tentative topics proposed for discussion include: The management, restoration, and creation of ecotones; the role of animals in ecotones; conservation of biological diversity in ecotones; and theoretical considerations, such as chaos theory and hierarchy theory. It is envisaged that, by the conclusion of the week-long symposium, a detailed programme of future field research projects will have been developed.

Long-term Collaborative Research Programme

Between November 1988 and May 1989 the research proposal will be distributed widely to interested research groups. Between May 1989 and January 1990 appropriate field stations will be identified, including a combination of Biosphere Reserves, Ramsar sites, NSF Long-Term Ecological Research sites, and IGBP Biosphere-Geosphere Observatories (see Dyer et al. 1988). These field stations will include examples of the various types of land/water ecotones described in this paper, and represent different climatic regimes. A series of workshops will be scheduled from 1991. Workshop discussions will determine the best locations for establishment of training courses and demonstration projects for managers of aquatic/terrestrial ecotones. It is envisioned that final data analysis and synthesis of reports will occur in 1995, with joint publication by MAB and IHP of recommendations for management of ecotones anticipated for 1996. During the early stages of this process efforts will be closely coordinated with the proposed SCOPE programme of symposia and workshops (Hansen et al. 1988b).

ACKNOWLEDGEMENTS

Many persons and agencies have contributed intellectually and monetarily to programme development. We thank F. Fournier, M. Hadley, G. Jolankai, M. Dyer, H. Loeffler, K. Hefny, E. Pieczynska, G. Pinay, F. Verhoog, H. Shugart, and J.-P. Ayrault for contributing their time and creative thoughts. Financial support was generously provided by the Programme Interdisciplinaire de Recherche sur l'Environnement (PIREN) of the Centre National de la Recherche Scientifique (France), UNESCO Man and the Biosphere Programme (MAB), United States - MAB, UNESCO International Hydrological Programme (IHP), the University of Minnesota, the College of New Rochelle (New York), the Scientific Committee on Problems of the Environment (SCOPE), and the International Institute of Applied Systems Analysis (IIASA).

LITERATURE CITED

Baudry, J. 1984. Effects of landscape structure on biological communities: the case of hedgerow network landscapes. Proceedings of the International Association of Landscape Ecology 1: 55-65.

Clements, F. E. 1905. Research methods in ecology. University Publishing Co., Lincoln, Nebraska, USA.

Correll, D. L., editor. 1986. Watershed Research Perspectives. Smithsonian Institution Press, Washington, D.C., USA.

Décamps, H., M. Fortuné, F. Gazelle and G. Pautou. 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landscape Ecology (submitted).

Décamps, H., J. Joachim and J. Lauga. 1987. The importance for birds of the riparian woodlands within the alluvial corridor of the River Garonne, S.W. France. Regulated Rivers 1: 301-316.

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science 179: 759-769.

Dyer, M. I., F. di Castri and A. J. Hansen, editors. 1988. Geosphere-Biosphere Observatories: Their definition and design for studying global change. Biology International, Special Issue 16.

Fitzpatrick, J. W. 1980. The wintering of North American tyrant flycatchers in the neotropics. Pages 67-78 _in_ J. A. Keast and E. S. Morton, editors. Migrant birds in the Neotropics: Ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Ford, T. E. and R. J. Naiman. 1988. Groundwater-surface water relationships in boreal forest watersheds: Dissolved organic carbon and inorganic nutrient dynamics. Canadian Journal of Fisheries and Aquatic Sciences (submitted).

Forel, F. A. 1892. Le Léman: monographie limnologique. F. Rouge. Lausanne, Switzerland.

Forman, R. T. T. 1981. Interaction among landscape elements: A core of landscape ecology. Proceedings of the International Congress of the Netherland Society of Landscape Ecology. Pudoc Wageningen: 35-48.

Forman, R. T. T. and M. Godron. 1981. Patches and structural components for a landscape ecology. BioScience 31 : 733-740.

Forman, R. T. T. and M. Godron. 1986. Landscape Ecology. John Wiley and Sons, New York, New York, USA.

Fortune, M. 1988. Historical changes of a large river in an urban area: The Garonne River in Toulouse. Regulated Rivers 2: (in press).

Franklin, J. F. and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. Landscape Ecology 1: 5-18.

Frissell, C. A., W.J. Liss, D. E. Warren and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environmental Management 10: 199-214.

Fustec, E., D. Pierre, T. Vallaeys, F. Coetil and J. Lauga. 1988. Les transferts de nitrates dans les nappes alluviales de la vallée de la Garonne (in preparation for Landscape Ecology).

Ghiselin, J. 1977. Analyzing ecotones to predict biotic productivity. Environmental Management 1: 235-238.

Goeden, G. B. 1979. Biogéographic theory as a management tool. Environmental Conservation 6: 27-32.

Hansen, A. J., F. di Castri and R. J. Naiman. 1988a. Ecotones: What and why? Biology International, Special Issue 17: 9-46.

Hansen, A. J., F. di Castri and P. G. Risser. 1988b. A new SCOPE project. Ecotones in a changing environment: The theory and management of landscape boundaries. Biology International, Special Issue 17: 137-163.

Hawkins, C. P. 1985. Substrate associations and longitudinal distributions in species of Ephemerellidae (Ephemeroptera : Insecta) from western Oregon. Freshwater Invertebrate Biology 4 : 181-188.

Hobbs, E. R. 1986. Characterizing the boundary between California annual grassland and coastal sage scrub with differential profiles. Vegetatio 65: 115-126.

Holland, M. M., Compiler. 1988. SCOPE/MAB technical consultations on landscape boundaries. Report of a SCOPE/MAB workshop on ecotones. Biology International, Special Issue 17: 47-106.

Holland, M. M. and D. J. Burk. 1982. Relative ages of western Massachusetts oxbow lakes. Northeastern Geology 4: 23-32.

Hollis, G. E., M. M. Holland, J. Larson and E. Maltby. 1988. Wise use of wetlands. Nature and Resources (in press).

Huet, M. 1949. Aperçu des relations entre la pente et les populations piscicoles des eaux courantes. Schweizerische Zeitschrift für Hydrologie 11: 333-351.

Huet, M. 1954. Biologie, profils en long et en travers des eaux courantes. Bulletin Français de Pisciculture 175: 41-53.

Illies, J. 1961. Versuch einer allgemeinen biozonotischen Gliederung der Fließgewasser. Internationale Revue der gesamten Hydrobiologie 46: 205-213.

Illies, J. and L. Botosaneanu. 1963. Problèmes et méthodes de la classification et de la zonation écologique des eaux courantes, considérées surtout du point de vue faunistique. Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 12: 1-57.

Jenkins, S. H. 1980. A size-distance relation in food selection by beavers. Ecology 61: 740-746.

Johnston, C. A. and R. J. Naiman. 1987. Boundary dynamics at the terrestrial-aquatic interface: The influence of beaver and geomorphology. Landscape Ecology 1: 47-57.

Johnston, C. A. and R. J. Naiman 1988. Browse selection by beaver: Effects on riparian forest composition. Ecology (submitted).

Keast, A., E. S. Morton, editors. 1980. Migrant birds in the Neotropics: Ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Lovejoy, T. E. 1979. Genetic aspects of dwindling populations: A review. Pages 275-279 in S. A. Temple, editor. Endangered birds: Management for preserving threatened species. University of Wisconsin Press, Madison, Wisconsin, USA.

Lovejoy, T. E., R. O. Bierragaard, Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubert and M. H. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 in M. E. Soulé, editor. Conservation biology: The science of scarcity and extinction. Sinauer Associates, Sunderland, Massachusets, USA.

McCoy, E. D., S. S. Bell and K. Walters. 1986. Identifying biotic boundaries across environmental gradients. Ecology 67: 749-759.

Merriam, G. 1984. Connectivity: A fundamental ecological characteristic of landscape pattern. Proceedings of the International Association of Landscape Ecology 1: 5-15.

Naiman, R. J., H. Décamps, J. Pastor and C. A. Johnston. 1988. The potential importance of boundaries to fluvial ecosystems. Oikos (in press).

Odum, W. E., T. J. Smith, J. K. Hoover and C. C. McIvor. 1984. The ecology of tidal freshwater marshes of the United States East Coast: A community profile. United States Fish and Wildlife Service FWS/OBS83/17. 177 pp.

Peterjohn, W. T. and D. L. Correll. 1984. Nutrient dynamics on an agricultural watershed : Observations on the role of a riparian forest. Ecology 65: 1466-1475.

Peterjohn, W. T. and D. L. Correll. 1986. The effect of riparian forest on the volume and chemical composition of base flow in an agriculture watershed. Pages 244-262 in D. L. Correll, editor. Watershed Research Perspectives. Smithsonian Institution Press, Washington, D.C., USA.

Petersen, R. C., B. L. Madsen, M. A. Wilzbach, C. H. D. Magadza, A. Paarlberg, A. Kullberg and K. W. Cummins. 1987. Stream management: Emerging global similarities. Ambio 16: 166-179.

Pickett, S. T. A. and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

Pinay, G. 1986. Relation sol-nappe dans les bois riverains de la Garonne. Etude de la dénitrification. These de Doctorat, Université Claude Bernard, Lyon, France. 198 pp.

Pinay, G. and H. Decamps. 1988. The role of riparian woods in regulating nitrogen fluxes between the alluvial aquifer and surface water: a conceptual model. Regulated Rivers 2 (in press).

Pringle, C., R. J. Naiman, R. Welcomme, M. Oswood, M. Winterbourn, G. Bretschko, J. Karr and J. R. Webster. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Oikos (in press).

Rast, W. and M. M. Holland. 1988. Eutrophication of lakes and reservoirs: a framework for making management decisions. Ambio (in press).

Risser, P. G., compiler. 1985. Spatial and temporal variability of biospheric and geospheric processes: research needed to determine interactions with global environmental change. The International Council of Scientific Unions Press, Paris, France.

Rzoska, J. 1978. On the Nature of Rivers with Case Stories of Nile, Zaire and Amazon. Dr. W. Junk bv Publishers, The Hague, Netherlands.

Sedell, J. R. and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: The isolation of the Williamette River, Oregon, U.S.A., from its floodplain by snagging and streamside forest removal. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 22: 1828-1834.

Shugart, H. H. 1984. A theory of forest dynamics. Springer-Verlag. New York, New York, USA.

Turner, M. G., editor. 1987. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.

UNESCO. 1986. Programme on Man and the Biosphere (MAB) General Scientific Advisory Panel. MAB Report Series Number 59, Paris, France.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Ward, J. V. and J. A. Stanford. 1988. Riverine ecosystems: The influence of man on catchment dynamics and fish ecology. Canadian Journal of Fisheries and Aquatic Sciences (in press).

Wetzel, R.G. 1975. Limnology. W.B. Saunder, Philadelphia, Pennsylvania, USA.

Wiens, J. A., C. S. Crawford and J. R. Gosz. 1985. Boundary dynamics: A conceptual framework for studying landscape ecosystems. Oikos 45: 421-427.

A NEW SCOPE PROJECT.
ECOTONES IN A CHANGING ENVIRONMENT:
THE THEORY AND MANAGEMENT OF LANDSCAPE BOUNDARIES

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Abstract. Ecotones, the transition zones between landscape elements, appear important in mediating the structure and functioning of ecological systems. Ecotones may act as differentially-permeable boundaries that influence the movements of energy, materials, and information across landscapes. They may also serve as primary habitats for species. SCOPE (Scientific Committee on Problems of the Environment) is proposing a new project on ecotones designed to enhance the development of ecological theory and improve land management. The project will examine the influence of ecotones on biodiversity and ecological flows, ecotonal responses to changes in the global environment, and the management of ecotones in a changing environment. A diverse array of scientists will be drawn together at a series of formal workshops and ad hoc assemblages to synthesize existing information, formulate theory, and develop management strategies.

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PROJECT RATIONALE

Human Impacts on the Biosphere

Mankind is now dramatically influencing the earth's climate and landscape structure at local, regional and global levels. Inappropriate land use practices in semi-arid areas are thought responsible for reductions in rainfall across regions (Walls 1980). The burning of fossil fuels is elevating atmospheric CO_2 and likely to result in global warming (Keeling et al. 1984, Manabe and Stouffer 1980). Furthermore, deforestation, agriculture, and urbanization are causing major changes in the types and abundances of terrestrial and aquatic habitats across continents. In many regions, natural habitats are being increasingly fragmented as anthropogenic habitats expand (e.g., Wilson 1984, Harris 1984). While in parts of Europe, agricultural lands have been abandoned and are now undergoing important changes in landscape boundary structure (Johnson and Corcelle 1987). The consequences of these human activities include desertification and loss of productivity in semi-arid regions (Walls 1980), loss of natural habitats such as wetlands and old-growth forests (Swift 1984, Harris 1984), accelerating rates of species extinctions (Ehrlich and Ehrlich 1981), possible coastal flooding through increases in sea level (Malone and Roder 1985), and alteration of landscape boundary structure (Holland, this issue). In total, these impacts on the biosphere are occurring at a rate probably exceeding that of any previous period since life arose (Malone and Roder 1985).

Designing strategies to mitigate these impacts is difficult because the linkages between climate, land use changes, and their ecological consequences are insufficiently understood. The International Geosphere-Biosphere Programme (IGBP) has been initiated to study these linkages (National Research Council 1986). Because interactions between various components of the landscape will often occur in the boundaries, research on ecotones need figure prominantly in the global change study. Ecotones may influence landscape dynamics by exerting control over the flow of energy, materials, and organisms between landscape elements. Ecotones also serve as habitat and may support unique patterns of biodiversity. Thirdly, ecotonal organisms and ecotonal systems are likely to respond dramatically to environmental change and, accordingly, it may be useful to monitor ecotones as early indicators of global change (Holland, this issue). Thus, studies on landscape boundaries offer the opportunity to better detect, understand, and manage global change.

For these reasons, the International Council of Scientific Unions' (ICSU) Scientific Committee of Problems in the Environment (SCOPE) is beginning a project on ecotones in the context of environmental change. The project will focus on: ecological flows and biodiversity associated with ecotones; responses of ecotones to global change; and landscape boundary management. This paper briefly examines each of these topics, explains the scientific focus of the SCOPE project, and describes the organizational structure of the project.

Ecotones and Ecological Flows

An important reason for studying ecotones relates to their strategic positioning between elements of a landscape. Natural and human disturbances cause most ecological systems to be patchy at several spatial and temporal scales (Pickett and White 1985). Most studies thus far have considered each landscape element or "patch" as a homogeneous unit and examined how patch size, shape, contagion, etc., influences several response variables including genetic variation, population dynamics, species diversity, energy flow, and nutrient cycling (see Mooney and Godron 1983, Sousa 1984, Pickett and White 1985 for reviews). The transition zones between patches (ecotones) may be particularly important in mediating the structure and functions of ecological systems (See also Hansen et al. 1988, Holland 1988, Naiman et al. 1988), especially by exerting control over the flow of materials, information, and energy between patches (Wiens et al. 1985, Johnson and Naiman 1987).

The extent to which landscape boundaries influence ecological flows is not well known and recent treatments of the topic remain speculative. Wiens et al. (1985) considered the factors that influence the spatial positioning of energy and materials across a landscape. They identified vectors (physical forces and animals) that can transport substances against underlying edaphic gradients. Wind, for example, may transport nutrients or organisms upslope. The trajectories of these vectors are affected by patch boundaries. The extent to which boundaries block or deflect the movements of vectors is expressed as boundary "permeability". Permeability is a function of both the characteristics of the boundary (e.g., width, position, physical structure) and the characteristics of the vectors (e.g., mobility, tolerance levels, within-patch density). By acting as filters of flows between patches, boundaries exert control over patch processes.

There is some empirical support for this conceptual model. Peterjohn and Correl (1984) monitored the movements of nutrients within a watershed containing croplands, riparian forest and a stream. The riparian forest was found to filter nitrogen and phosphorus from both groundwater and surface runoff. The forest retained 89 % and 80 % of the total N and P inputs respectively, while the cropland retained only 8 % and 41 % respectively. The ecotonal vegetation, thus, was relatively impermeable to solutions of these nutrients and inhibited their movement into the stream.

Ecotones may also influence the spread of disturbance. A network of ecotones that is resistant to particular disturbance sometimes reduces the size/frequency distribution of that disturbance regime. Odum et al. (1987) examined the consequences of the construction of sand dunes along the seaward sides of barrier islands on the coast of North Carolina (U.S.A.). The artificial dunes appear to have impeded ocean flooding and salt spraying across the islands. This change in the disturbance regime (along with artificial planting and fertilization of dune-stabilizing plants) strongly influenced adjacent plant communities. Compared with natural islands, the managed islands were: higher in biomass, vegetative cover, plant litter ; lower in diversity; and supported a greater expansion of shrubs. Alternatively, ecotones that promote the spread of disturbance are probably not uncommon. For example, coniferous forests nature trees bordering early successional vegetation are more subject to windthrow than those in forest interiors (Sprugel 1976, Franklin and Forman 1986).

Patch boundaries may vary in permeability to animal movements. Canopy birds are more likely to descend into forest gaps if the gaps edges are gradual rather than abrupt (Wunderle et al. 1987). Also, Gates and Gysel (1978) found that predation on passerines eggs and nestlings was highest near forest/field edges, possibly these ecotones function as barriers that cause predators to move parallel to the edges.

The studies described above indicate that some ecotones exert control over flows between ecological systems and in doing so influence patch functioning. The generality of this effect is not presently known. More research on the topic may well improve our understanding of the interactions between landscape components and have important implications for the management of disturbance and other ecological flows.

Biodiversity and Ecotones

The study of biotic diversity in ecotones has even more direct implications for management. The rate of species extinction has dramatically accelerated in recent decades, largely due to habitat alterations by man (Ehrlich and Ehrlich 1981). Reductions in genetic variability and local extripation of species, though poorly quantified, are probably even more prevalent. The value of maintaining biotic diversity has been analyzed on medical, agricultural, ecological, and aesthetic grounds (See Wilson 1984).

A problem related to the loss of some species is an undesirable increase in the abundance of others. Ruderal species (sensu Grime 1979) are particularly apt to invade a region following human disturbance and become pests (Crawley 1987). The phenomenom is surprisingly common (Crosby 1986) and the economic losses due to pest species is extremely high. Less well known are the ecological costs in terms of the displacement of native species or the destabilization of ecological processes (Mooney and Drake 1986).

Species rarity and overabundance are often related to landscape structure and, in particular, to boundary characteristics. Wildlife managers have long recognized that some types of ecotones support high diversity and abundance of vertebrates (Leopold 1933, Dasmann 1964). This "edge effect" is not universal, however. Ecotones subject to high levels of disturbance (e.g., the edges of unstable water bodies) may be poor in species (van der Maarel 1976). Furthermore, the creation of habitat edges may reduce regional diversity because patch interior species are lost (Noss 1983).

The relationships between landscape structure and species abundance are often complex and involve several organizational levels. A conceptual model of these linkages is presented in Figure 1. According to the model, disturbances and other environmental fluctuations (agents of change) either influence population demography directly by injuring or killing individuals or act indirectly by altering landscape structure. The complex of resource patches, habitats, corridors, and barriers that comprise the landscape (Forman and Godron 1986) provide a context that varies in suitability for each species. Species abundance may vary accordingly. Demography is also influenced by internal control. The genetic structure of the population and the environment interact to produce a population phenotype, or life history strategy, which sets the limits for demographic parameters such as rate of increase or size structure (Gilpin and Soulé 1986). Consideration of genetics is especially important for small populations because inbreeding and genetic drift are more likely reducing population fitness (Thompson 1985, Allendorf and Leavy 1986).

Agents of change such as deforestation may reduce the habitat of a species to small, isolated patches that can support only small populations. Genetic drift or inbreeding may then lower the fitness of the population and elevate the risk of extinction (Vrijenhoek 1985). Alternatively,

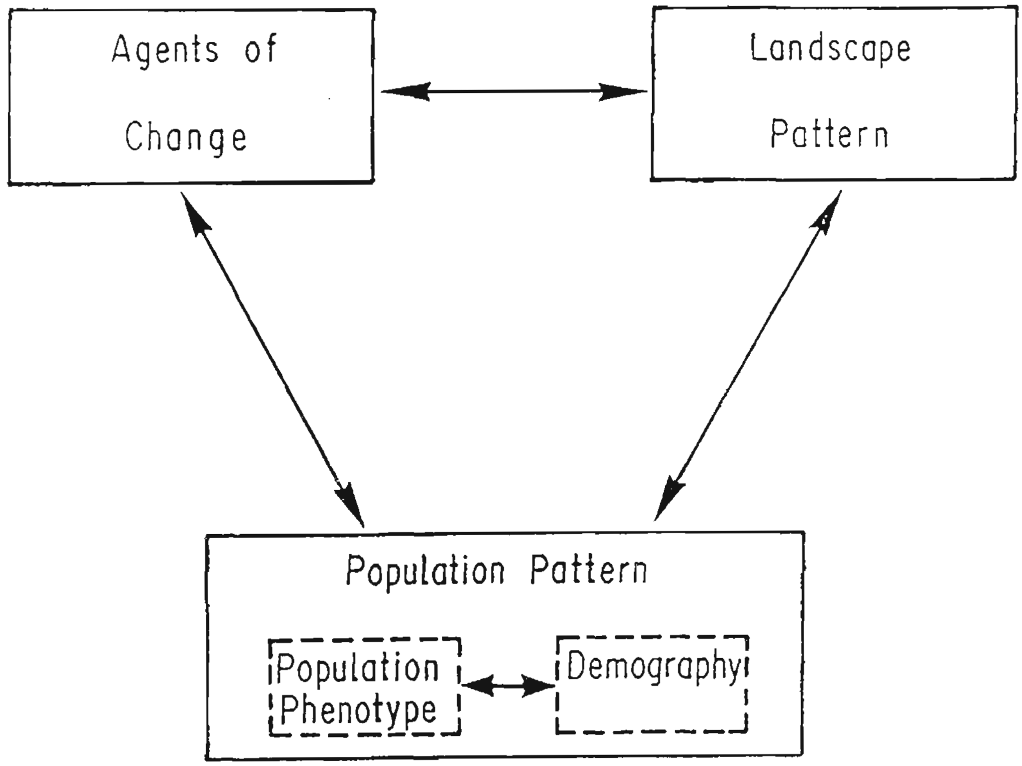

Figure 1. Conceptual model of the relationships among factors that influence the abundance of a species. "Agents of Change" refers to environmental fluctuations and disturbances (Hansen and Walker, 1985). See text for further explanation.

environmental events that enhance habitat connectivity may allow some species to become overabundant and invasive. Such species may themselves be agents of change that alter landscape pattern or the demography of other species.

It appears, thus, that these are important linkages between landscape boundary structure and biodiversity. Research is needed to assess how these linkages are influenced by natural agents of change and the extent to which human-induced change will modify these relationships. Clearly, this work will require investigation at several levels of organization including the genetic, population, and landscape levels.

Ecotones as Indicators of Global Change

The IGBP is designed to coordinate hydrologic, atmospheric and terrestrial research on biospheric impacts of human activities (National Research Council 1986). Changes in global state variables such as reflectivity or atmospheric temperature are expected to induce responses in vegetation. These responses may be particularly acute at landscape boundaries and hence there is considerable interest in monitoring ecotones to assess the dynamics of global state variables. The rationale is that many organisms experience severe limitations in the transition zones between communities. Accordingly, changes in environmental conditions should be rapidly manifest as changes in the location or characteristics of ecotones (Solomon 1986).

Monitoring ecotones to assess global change will require innovative methodological approaches. Measurements need be made over a broad range of spatial and temporal scales (National Research Council 1986), perhaps by using remote sensing to supplement ground-based methods (See Dyer and Crossley 1986). With this technology ecologists can, for the first time, collect data at a variety of scales: from coarse spatial scales and high temporal resolutions to fine spatial scales and low temporal resolutions. Although few, if any, remote sensing studies have focused exclusively on ecotones, a growing collection of vegetation studies have been completed.

These range from monitoring primary plant productivity and seasonality across entire continents (eg. Tucker and Sellers 1986, Goward et al. 1986) to mapping units within regions (White and Mac Kenzie 1986).

The approach is not without limitations at the present time (Lacaze, personal communication). Cloud cover often results in unacceptably low temporal frequency. Overlapping spectral reflectance among plant species or communities often makes vegetation mapping difficult. And thirdly, it is often difficult to link the fine-scaled, many-variable data sets of field studies with the larger-scale, few variable data sets from satellite imagery. Despite these limitations, use of remote sensing technology for monitoring ecotones seems fertile ground for research.

SCIENTIFIC FOCUS OF PROJECT

The SCOPE ecotones project will examine patterns and processes of biodiversity and ecological flows associated with ecotones, especially under the influence of natural and anthropogenic agents of change. Specific objectives are as follows:

1. Review and synthesize existing information on the patterns and processes of :
   (a) genetic, species, and landscape diversity in ecological system boundaries ;
   (b) material, energy, and genetic information flows across ecological boundaries.
2. Assess the susceptibility of organisms and ecotones to environmental change, especially at the global level.
3. Evaluate ecotones as early indicators of global change.
4. Formulate mathematical models for understanding and managing ecotones.
5. Develop management strategies and techniques for optimizing landscape characteristics.

In order to achieve these objectives, three general questions will be explored.

First, how do ecological system boundaries influence biotic diversity and the flows of energy, information, and materials ? The patterns of diversity and ecological flows will be described in landscapes of differing boundary structure. The mechanisms underlying these patterns and their consequences relative to system functioning will then be analyzed. These topics will be examined at various organizational levels in order to clarify the relationship between genetic, population, and landscape processes. The effects of natural disturbance and other agents of change will be explicitely considered. Important ancillary topics such as the classification of ecotones and the history of human impacts on landscape structure will also be addressed.

Second, how will biodiversity and ecological flows associated with ecotones respond to environmental change, especially in global climate, sea level, land use, and atmospheric trace gases ? The focus here is on the ways in which the relationships between landscape structure, biodiversity, and ecological flows are being altered by human activity, especially activities that cause change at the global level. The project will investigate which types of species and ecological systems are most susceptible to change as a consequence of human disturbance. In the case of organisms, susceptibility refers not only to the likelihood that a species will become rare, but also the possibility that it will become overabundant and invasive. Studies of the sensitivity of ecotones to environmental change are also important and the project will evaluate the feasibility of monitoring ecotones as early indicators of global change.

Third, how should ecotones be managed within a changing environment ? Given that man is now capable of impacting the biosphere, we need the knowledge and the techniques to maintain or create suitable or optimal landscape patterns within the context of environment change. The final phase of the SCOPE project will involve integrating the results of previous project activities to develop strategies and techniques for landscape management.

These three questions will be examined by reviewing and synthesizing existing information, not via field research. Scientists from diverse disciplines will integrate previous studies, evaluate current theory, develop new theory, construct mathematical models, and generate management approaches. These activities will take place primarily during formal workshops and meetings of small ad hoc working groups.

PROJECT STRUCTURE

The lion's share of the project activities will revolve around three semi-independent workshops (Table 1). Each will be unique in terms of general scientific questions, organizational and editorial directorship, location, and final product. The workshops will be linked, however, in that the product of one will be the point of departure for the next. Additionally, three ad hoc working groups will assemble and give special attention to the classification of ecotones, human impacts on landscape structure, and mathematical approaches for studying and managing ecotones. The project will continue for three years and culminate with a final synthesis meeting.

The workshops will have a standard format. Approximately 25 scientists will attend at each 4-5 day meeting. Plenary papers will be offered first. Working groups will then convene individually, present short working papers on specific topics, discuss and analyse the topics at hand, and report back to the plenary session. The workshops will close after a period for synthesis and reassessment of future goals and activities. The participants will be selected based on their expertise in the specific topics to be examined. For the sake of project coherence and continuity, some scientists will participate in all three workshops; others will attend only one or two.

Workshop I - Biodiversity, Ecological Flows, and Ecotones

The first workshop will examine the patterns of biodiversity and ecological flows associated with patch boundaries, the mechanisms underlying these

Table 1. **Overview of activities planned for SCOPE project on ecotones.**

Attribute	Activity					
	Workshops I	Workshops II	Workshops III	Special Papers	International Working Group	Synthesis
Subject	Influence of ecotones on biodiversity and ecological flows	Relationships between ecotones and global change	Management of ecotones within a changing environment	1 Classification of ecotones 2 Human impacts on landscape structure	Mathematical approaches for ecotone research and management	Integration of all project activities
Format	4-day meeting with plenary papers and working groups	4-day meeting with plenary papers and working groups	4-5 day meeting with plenary papers and working groups	To be decided by National Committees	Two informal work sessions of 2-4 days each	4-day interactive technical consultation
Number of Participants	25	25	25	To be decided by National Committees	3-4	15
Date	September 1988	May 1989	October 1989	January 1988 to January 1989	June 1988 to September 1989	March 1990
Location *	France	USA	USSR	To be decided by National Committees	Austria	Austria
Products	Commercially published book	Commercially published book	Commercially published book	Scientific journal articles	Scientific journal articles	Book for SCOPE Series by John Wiley & Sons

* Locations are tentative, based upon eventual funding sources.

patterns, and their consequences for system functioning. It will be basic in approach and focus primarily on landscapes subject to natural agents of change. The main objective is to review empirical information and improve current theory on biodiversity and flows in ecotones that are not strongly influenced by human activities.

Workshop I will open with plenary papers that review current knowledge on the structure, function, and classification of ecotones and patterns of diversity, and ecological flows associated with ecotones (Table 2). One study group will then concentrate on biodiversity at various organizational levels and the other on ecological flows within and across boundaries. The two groups will then reunite to discuss the commonalities and differences in these two related topics. It is expected that this interaction between evolutionary biologists and community ecologists will clarify the links between genetic, population, and landscape processes. The workshop will end with a plenary session on the possible contributions ecotones research can make to the International Geosphere-Biosphere Program on global change.

Workshop II - Human Impacts on Ecotones

Workshop II will focus on the influences of human-induced environmental change on biodiversity and flows at ecotones, especially changes in global climate, sea level, land use, and atmospheric trace gases. One goal is to assess which species and which ecological systems are most susceptible to such changes and the factors that underlie this sensitivity. Another goal is to evaluate the usefulness of monitoring ecotones as early indicators of global change.

The initial plenary papers will review current predictions on global change and previous research on organism and ecotone susceptibility to and influence on global change (Table 3). The study groups will analyse these topics in greater detail. The meeting will conclude with discussion on methodologies and facilities required for monitoring interactions between ecological boundaries and global change parameters.

Table 2. **Tentative contents of Workshop I on biodiversity and ecological flows associated with ecotones.**

<table>
<tr><th></th><th colspan="2">Morning</th><th>Afternoon</th></tr>
<tr><td>Day I</td><td colspan="2"><u>Plenary Papers</u>

Introduction

Classification of Ecotones

Human Impacts on Ecotones</td><td><u>Plenary Papers</u>

Structure of Ecological Boundaries

Processes in Ecotones

Biodiversity

Ecological Flows</td></tr>
<tr><td rowspan="2">Day II</td><td colspan="2"><u>Concurrent Working Group Papers</u></td><td rowspan="2">Concurrent Working Sessions

Plenary Reviews</td></tr>
<tr><td><u>Diversity</u>
Genetic Level
Species Level
Landscape Level</td><td><u>Flows</u>
Within Ecotones
Through Ecotones</td></tr>
<tr><td>Day III</td><td colspan="2">Concurrent Working Sessions

Summary within Groups</td><td>Open</td></tr>
<tr><td>Day IV</td><td colspan="2">Working Group Reports

Parameters for Monitoring Ecotones</td><td><u>Synthesis</u>

Expectations for Global Change

Future Questions and Research on Ecotones and Global Change</td></tr>
</table>

Table 3. **Tentative schedule for Workshop II on organism and ecotone response to and influence on global change.**

	Morning	Afternoon
Day I	Plenary Papers Project Objectives and Summary of Workshop I Organism and Ecotone Susceptability to and influence on Global Change	Plenary Papers Predictions on Global Change concerning Climate, Land Use, Sea Level, Air Pollution and Extreme Events
Day II	Concurrent Working Group Papers Biodiversity: Susceptability to and Influence on Global Change Flows: Susceptability to and Influence on Global Change	Concurrent Working Sessions Plenary Reviews
Day III	Concurrent Working Sessions Summary within Groups	Open
Day IV	Working Group Reports Use of Models Needs for Biospheric Observatories	Synthesis Future Questions and Research on Ecotones and Global Change

Workshop III - Managing Ecotones

Within the context of a changing environment, how should ecotones be managed ? To what extent can susceptible species or ecotonal systems be stabilized, preserved, or restored to maintain or create optimal landscape characteristics ? These questions will be the foci of the third workshop. The precise contents of the meeting are contingent upon the outcome of Workshops I and II and early developments in IGBP. Tentatively, the plenary session will open with a review of the previous consultations (Table 4). A retrospective analysis will then compare recent human impacts on landscape structure with the longer-term, historic relationships between the development of civilizations and landscape characteristics. Other plenary topics will include conservation strategies and techniques, mathematical models useful for management, the rationale and process of monitoring ecotones.

One study group will discuss strategies and techniques for the conservation, restoration, and creation of ecotones. Innovative approaches will be examined such as "bioengineering" ecotones, alterating species composition or vegetative structure to attain specific goals. One such goal may be inhibiting certain species from becoming overabundant and invasive. The "canary" approach of monitoring sensitive species as early warning signs of environmental change will also be explored. The genetic variability, productivity, or population dynamics of various plant or animal species may be good indicators of specific environmental changes, and in addition, specific characteristics of ecotones may also be sensitive indicators.

The other study group will deal with mathematical modeling as a management tool. The need is apparent for multi-scale models that simulate and couple processes at various organizational levels. The goal of the modeling effort is to analyse ways of improving landscape characteristics vis-à-vis ecotone management.

Table 4. **Tentative contents of Workshop III involving managing ecotones in a changing environment.**

	Morning	Afternoon
Day I	Plenary Papers Results of Workshop I and II Retrospective Analysis of Human Interactions with Landscape Structure	Plenary Papers Conservation Strategies Models for Management Rationale and Techniques for Management
Day II	Concurrent Working Group Papers Conservation Strategies and Techniques: Bioengineering of Ecotones; Ecotones characteristics as indicators of change Management Models: Multiple-scale Models; Landscape Optimization	Concurrent Working Sessions Plenary Reviews
Day III	Concurrent Working Sessions Summary within Groups	Open
Day IV	Working Group Reports	Regional Examples
Day V	Synthesis Future Prospects for Research and Management	Open

The working group reports will be followed by plenary papers that offer regional examples of ecotone management in a range of biomes including those in humid tropics, seasonally-arid subtropics, temperate zones, cold zones, and wetlands. The workshop will end with discussion on the synthesis of regional and global management approaches.

Ad Hoc Working Groups

Two topics of study are identified as meriting special attention early in the ecotones project: classification of ecotones and human impacts on landscape patterns. Consideration of the first is essential for the development of theory on ecotones and the latter has direct implications for landscape management. Groups of 3-4 scientists will be convened by SCOPE National Committees to prepare in-depth special papers on each of these subjects and present them in the plenary session of Workshop I.

Additionally, an international working group will be organized on mathematics and modeling. Various mathematical approaches appear potentially useful for the study of ecological system boundaries. These include fractal geometry, (Loehle 1983), diffusion models (Okubu 1980), hierarchy theory (O'Neill et al. 1986), catastrophy theory (Poston and Stewart 1978), and spatial autocorrelation (Ripley 1978). The ad hoc working group of three or four scientists will evaluate the applicability of these techniques for ecotone research and management. The group will report their findings at Workshop III.

Synthesis

The project will conclude with a synthesis meeting. Key participants in the project will draw together all of the information and materials generated during the project for integration into a concise, state-of-the-art account of the theory and management of ecotones in a changing environment.

Cooperation with Other Programs

A key to a successful SCOPE project on ecotones will be the close interaction and cooperation with other scientific groups that are addressing problems on landscape patterning and environmental change. Studies that are especially pertinent to this one include: the SCOPE project on ecosystem experiments; the UNESCO project on Inland-water/land ecotones(Naiman et al. 1988); the IGBP assessment of facilities needed for monitoring global change (Dyer et al. 1988); and various other aspects of IGBP. Representatives of these projects will be asked to contribute to the SCOPE workshops on ecotones for facilitating exchanges of ideas and information.

ACKNOWLEDGEMENTS

Many of the ideas presented here were initiated by participants of the SCOPE/MAB Technical Consultation on Ecotones held in Paris, France in January 1987. The present form of the project was developed at a recent meeting of SCOPE Advisory Committee on Ecotones sponsored by the International Institute for Applied Systems Analysis (IIASA) in Laxenburg, Austria. Names of participants are listed in Appendix 1. T. Munn and S. Wilson of IIASA organized meeting logistics. This work was made possible by support from the Carnegie-Mellon Foundation and the Centre Louis Emberger, C.N.R.S., Montpellier, France. We offer thanks to all of these individuals and organizations.

LITERATURE CITED

Allendorf, F. W. and R. F. Leavy. 1986. Heterogeneity and fitness in natural populations of animals. Pages 57-76 in M. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Crawley, M. J. 1987. What makes a community invasiable? Pages 429-453 in A. J. Gray, M. J. Crawley and P. J. Edwards, editors. Colonization, succession and stability. Blackwell Scientific Publications, Oxford, UK.

Crosby, A. W. 1986. Ecological imperialism. The biological expansion of Europe, 900-1900. Cambridge University Press, Cambridge, UK.

Dasmann, R. F. 1964. Wildlife biology. John Wiley and Sons, New York, New York, USA.

Dyer, M. I. and D. A. Crossley. 1986. Coupling of ecological studies with remote sensing: Potentials at four biosphere reserves in the United States. U.S. Man and Biosphere Program. Washington, D.C., USA.

Dyer, M. I., F. di Castri and A. J Hansen. 1988. Geosphere-Biosphere Observatories: Their definition and design for studying global change. Biology International, Special Issue 16.

Ehrlich, P. R. and A. H. Ehrlich. 1981. Extinction: The causes and consequences of the disappearance of species. Random House, New York, New York, USA.

Forman, R. T. T. and M. Godron. 1986. Landscape ecology. John Wiley and Sons, New York, New York, USA.

Franklin, J. F. and R. T. T. Forman. 1986. Influences of patch clearcutting on potential for catastrophic disturbance in coniferous forest landscapes of the Pacific Northtwest. Symposium Presentation: The role of landscape heterogeneity in the spread of disturbance. University of Georgia. Athens, Georgia.

Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59: 871-883.

Gilpin, M. E. and M. E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pages 19-34 in M. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Goward, S. N., C. J. Tucker and D. G. Dye. 1986. North American vegetation patterns observed with meteorological satellite data. Pages 96-115 in M. I. Dyer and D. A. Crossley, editors. Coupling of ecological studies with remote sensing: Potential at four biosphere reserves in the United States. U.S. Man and the Biosphere Program. Washington, D.C., USA.

Grime,J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York, New York, USA.

Hansen, A. J. and B. H. Walker. 1985. The dynamic landscape: Perturbation, biotic response, biotic patterns. S. African Inst. Ecol. Bull. 4: 5-14.

Hansen, A. J., F. di Castri and R. J. Naiman. 1988. Ecotones: What and why? Biology International, Special Issue 17: 9-46.

Harris, L. 1984. The fragmented forest. University of Chicago Press, Chicago, Illinois, USA.

Holland, M. M., Compiler. 1988. SCOPE/MAB technical consultation on landscape boundaries. Report of a SCOPE/MAB workshop on ecotones. Biology International, Special Issue 17: 47-106.

Johnson, S. and G. Corcelle. 1987. L'autre Europe "verte": La politique communautaire de l'environnement. Editions LABOR, Bruxelles, Bèlgium.

Johnston, C. A. and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landscape Ecology 1: 47-57.

Keeling, C. D., A. F. Carter and W. G. Mook. 1984. Seasonal, latitudinal, and secular variations in the abundance and isotopic ratios of atmospheric CO_2. J. Geophys. Res. 89: 4615-4628.

Leopold, A. 1933. Game management. Schriber, New York, New York, USA.

Loehle, C. 1983. The fractal dimension and ecology. Speculations in Science and Technology 6: 131-142.

Malone, T. F. and J. G. Roeder. 1985. Global change. Cambridge University Press, Cambridge, UK.

Manabe, S. and R. J. Stouffer. 1980. Sensitivity of a global model to an increase of CO_2 in the atmosphere. J. Geophys. Res. 85(C10): 5529-5550.

Mooney, H. A. and M. Godron. 1983. Disturbance and ecosystems. Springer-Verlag, New York, New York, USA.

Mooney, H. A. and J. Drake. 1986. The ecological consequences of biological invasions. Springer-Verlag, New York, New York, USA.

Naiman, R. J., M. M. Holland, H. Décamps and P. G. Risser. 1988. A new UNESCO programme: Research and management of land/inland water ecotones. Biology International, Special Issue 17: 107-136.

National Research Council. 1986. Global change in the geosphere-biosphere. National Academy Press, Washington, D.C., USA.

Noss, R. F. 1983. A regional landscape approach to maintain diversity. BioScience. 33: 700-706.

Odum, W. E., T. J. Smith and R. Dolan. 1987. Suppression of natural disturbance: Long-term ecological change on the Outer Banks of North Carolina. Pages 123-135 in M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.

Okubo, A. 1980. Diffusion and ecological problems: Mathematical models. Biomathematics 10: 1-254.

O'Neill, R. V., D. L. De Angelis, J. B Waide and T. F. H. Allen. 1986. A hierarchical concept of the ecosystem. Princeton University Press, Princeton New Jersey, USA.

Peterjohn, W. T. and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. Ecology 65: 1466-1475.

Pickett, S. T. A. and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press., Inc., New York, New York, USA.

Poston, T. and J. Stewart. 1978. Catastrophe theory and its applications. Pitman, London, UK.

Ripley, B. D. 1978. Spectral analysis and the analysis of pattern in plant communities. J. Ecol. 66: 965-981.

Risser, P. 1987. Landscape ecology: State of the art. Pages 3-14 in M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.

Solomon, A. M. 1986. Transient response of forests to CO_2-induced climate change: Simulation modeling experiments in eastern North America. Oecologia (Berlin) 68: 567-579.

Sousa, W. 1984. The role of disturbance in natural communities. Ann. Rev. Ecol. System. 15: 535-591.

Sprugel, D. G. 1976. Dynamic structure of wave generated Abies balsamea forest in the northeastern United States. J. Ecology 64: 889-911.

Swift. 1984. Status of riparian ecosystems in the United States. Water Research Bulletin 20: 223-228.

Thompson, J. N. 1985. Within-patch dynamics of life histories, populations and interactions: Selection over time in small spaces. Pages 253-264 in S. T. A. Pickett and P. S White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., New York, New York, USA.

Tucker, C. J. and P. J. Sellers. 1986. Satellite remote sensing of primary production. Int. J. Remote Sensing 7: 1395-1416.

Urban, D. L., R. V. O'Neill and H. H. Shugart. 1987. Landscape ecology: A hierarchical perspective can help scientists understand spatial patterns. BioScience 37: 119-127.

van der Maarel, E. 1976. On the establishment of plant community boundaries. Ber. Deutsch. Bot. Ges. Bd. 89(5): 415-443.

Vrijenhoek, R. C. 1985. Animal population genetics and disturbance: The effects of local extinctions and recolonizations on heterozygosity and fitness. Pages 266-286 in S. T. A Pickett and P. S White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., New York, New York, USA.

Walls, J. 1980. Land, man, and sand: Desertification and its solution. Macmillan Pubs., New York, New York, USA.

White, P. S. and M. MacKenzie. 1986. Remote sensing and landscape pattern in Great Smoky Mountains Park Biosphere Reserve, North Carolina and Tennessee. Pages 52-70 in M. I. Dyer and D. A. Crossley, editors. Coupling of ecological studies with remote sensing: Potential at four biosphere reserves in the United States. U.S. Man and the Biosphere Program. Washington, D.C., USA.

Wiens, J. A., C. S. Crawford and J. R. Gosz. 1985. Boundary dynamics: A conceptual framework for studying landscape ecosystems. Oikos 45: 421-427.

Wilcove, D. S., C. H. McLellean and A. P. Dobson. 1986. Habitat fragmentation in the Temperate Zone. Pages 237-256 in M. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Wilson, E. O. 1984. Biophilia. Harvard University Press, Cambridge, Massachusetts, USA.

Wunderle, J. M., A. Diaz, I. Velazquez and R. Schawon. 1987. Forest openings and the distribution of understory birds in a Puerto Rican rainforest. Wilson Bull. 99: 22-37.

Appendix I. **Participants in the planning meeting of the SCOPE Scientific Advisory Committee on Ecotones held at the International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria, on September 7-9, 1987.**

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