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Notes on ecotone attributes and functions

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Abstract

We attempt to identify general properties of ecotones. Earlier attempts to do so encountered difficulties resulting from contradictory conceptions of ecotones. Thus, we begin with and center our discussion on a definition of ecotone. The definition is complex. It includes scaling, structural, and functional aspects. Based on this complex definition, we offer a brief review of what is an ecotone, what attributes it has, and how it influences other habitats of interest. We identify feedback as a possibly important but ignored function of ecotones. This discussion is presented in general terms which apply to a variety of ecological situations. We point out that results of an evaluation of ecotone attributes largely depends on the spatial and temporal scale at which ecotone is conceptualized and data are collected. We suggest that some of ecotone determinants scale naturally in a repeatable fashion among various aquatic systems. Finally, we point to the concentration of dynamic properties of ecotones as applied to land/water interface.

Introduction

Research on the role of ecotones in aquatic and terrestrial systems has acquired considerable momentum during the last five years. Conceptual developments have generally kept pace with the empirical studies. These developments have been refined to the point that new fundamental problems and opportunities have become apparent. We need to discuss these.

One problem, important both to research on lotic ecotones and to general understanding of ecology, is the relation between spatial (ecotones) and functional (ecosystems) attributes of ecological fabric. Shugart (1990) articulated an important conceptual inconsistency in one common definition of ecotone (if one interprets that definition in a particular way). He argues that if an ecotone is a boundary between ecosystems, and ecosystems are bounded in arbitrary ways, then ecotones would also be arbitrary. Indeed, studying arbitrary objects is ineffective because it relies on finding natural regularities by chance rather than in a systematic way. A definition by Holland (1988) removes this difficulty but creates another. According to Holland (1988) an ecotone is a zone of transition between adjacent ecological systems such as uniform macrophyte stand and open water. The problem arising here is that functional approaches to ecological systems originally developed around the ecosystem concept that do not require uniformity of appearance as postulated by Holland's definition. A watershed ecosystem, or a lake, is far from being uniform. These logical and terminological inconsistencies are important because they interfere with the evaluation of the role of ecotones in the maintenance of integrated, sustainable associations of organisms. Informal and inconsistent approaches are particularly confusing when cross-system comparisons are the goal (e.g., Downing, 1991). We feel however that there is a good possibility for reconciliation of the functional, dynamic perspective and the spatial aspect embodied in the ecotone concept.

We propose that such reconciliation will be best accomplished by a more systematic examination of the ecotone as concept. This examination, as it applies to fish ecology, is a major goal of this paper. Several recent publications are particularly helpful in this regard. We will intensively use and rely on the experience and ideas assembled in Naiman *et al.* (1992), Naiman & Décamp (1990), Hansen & di Castri (1992), and Zalewski *et al.* (1991). In our view status of a habitat as ecotone differs depending on the spatial scale considered. This, in turn, depends on the prior delineation of the system of interest. Such delineation is a necessary basis for asking valid research questions (Kolasa & Pickett, 1989; Kolasa & Rollo, 1981). If, as it may be the situation in some cases, the delineation coincides with multiple ecological discontinuities (cf. Shugart, 1990), then the ecotone is a 'boundary of the system' such as an ecosystem, population, or species assemblage. If, however, discontinuities appear on the inside of the system of interest, then ecotone becomes a 'part of that system'. Such a part may be linear or reticulate in shape and is defined by an abrupt change in parameter values when one measures them across it. This is simpler than it sounds. For example, let our system be a river drainage basin. Here individual branches of the river separate, most of the time, identical habitats. When viewed at this large scale, they are not boundaries. Such ecotones form the fabric of a larger system. When viewed at a scale of tens of meters, each branch or tributary appears associated with two parallel shoreline ecotones. These ecotones are boundaries (between the water course and adjacent patches of terrestrial habitats). The distinction in ecotone status with respect to the system is important. It is so if we wish to compare various ecotones and their role in ecology of freshwaters, and fish in particular, among various settings, geographical regions, and habitats. For example, one might need to apply different methods and interpretation to ecotones that are part of a system compared to ecotones that are boundaries. We intend to combine this scaled perspective with some ideas recently developed by others and add a few of our own.

We organize the discussion into various areas. Separately, we focus on the identification of ecotones, their function, and the aspects of ecotone study.

Ecotone morphology and anatomy

Ideally, an ecotone can be represented as a straight habitat band between two other adjacent habitats (Fig. 1A, upper left panel). The reality is always more complex and the spatial complexity of an ecotone (as a transitional zone) has at least two aspects: sinuosity and resolution.

The sinuosity aspect refers to the degree of the band contortion and fragmentation (Fig. 1A, from left to right). As the sinuosity increases, (i) the total length of the ecotone relative to either habitat increases, (ii) the width of the ecotone increases and, (iii) the nature of the ecotone changes. In the first panel it was a simple band or transition zone. In the third panel it becomes a new and wider transition zone consisting of a mosaic of patches, including the original transition zone habitat as well as patches of the two habitats that originally formed that transition zone. This widening of ecotone and increase in ecotone complexity are identified by brackets at the bottom of the panels (Fig. 1A). Indeed, for each ecotone identified at these different scales it is possible to identify, analyze and compare attributes represented in Fig. 1B and 1C (see below).

The resolution aspect identifies spatial scale at which ecotone appears. For example, a patch of the ecotone habitat (Fig. 1A; right panel) has itself an ecotone with the open water habitat at a smaller spatial scale. However, this new scaled down ecotone differs in many respects. If the large scale ecotone was a zone of macrophytes along a river or lake shore, the small scale ecotone may be the outer edge of this zone, with greater water exchange, higher light and nutrient availabilities, and greater hydraulic energy conditions. Both scales may interact in a variety of ways. The simplest would be a positive correlation between the total lengths of ecotones observed at each scale. For example, doubling the length of the ecotone at one scale may mean quadrupling the total length of ecotone at a lower scale. Naiman *et al.* (1988) analyze and illustrate various consequences of scale and habitat hierarchy in greater detail, including the predictability of states. Some scales and some ecotones have been long recognized and measured. Shore development index (e.g., Hutchinson, 1957) is a good example of standard procedure used to summarize spatial properties of the lake shores and can be used to quantify one scale of terrestrial aquatic ecotones. Interactions among various scales have not been given much attention but may be important to many vertebrate and invertebrate species that use land/water interface. For example, the edge diversity index applied to wetland vegetation (Harris *et al.* 1983) would be greatly affected by the choice of resolution even though in each case it would describe some properties of ecotones. Indeed, while which resolution is selected and quantified depends on a research question, existence of ecotones at different scales does not.

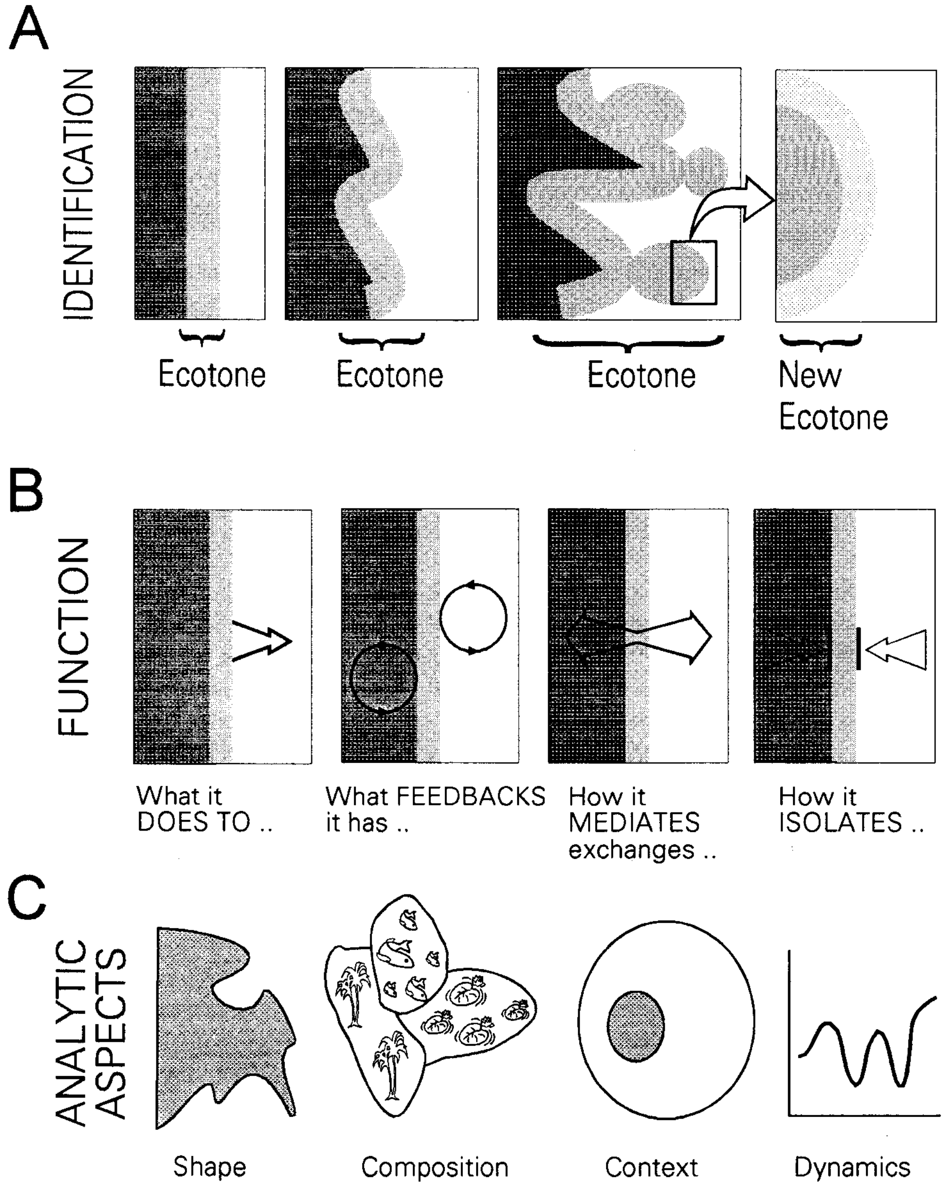

Fig. 1. A pictorial definition of ecotone. A – the scale dependence of the concept; the ecotone width changes with its shape and the change in shape may be associated with a change in composition, *i.e.*, the third diagram from the left includes 'dark', 'grey' and 'white' habitat types. B – the range of interactions (commonly referred to as functions) an ecotone may have with other habitats; the functions include, from left to right, directional impacts, feedbacks, modifications of flows or processes, and isolation or filtering out of processes. C – principal properties of ecotones that require systematic attention and specification include ecotone morphology, composition, embedding or context, and temporal behaviors. See text for the detailed discussion.

It is important to note that, while habitat identified as ecotone has in nature a third spatial dimension-height, that dimension is not a part of the ecotone delineation. This third dimension may become an important factor, however, when ecotone function is analyzed (see next section).

Finally, the temporal dimension should not be ignored any further. Identification of an ecotone depends on the time over which the interactions of two habitats are observed. A transition zone between land and water varies at the scale of days, seasons, years, and decades. A riverine ecotone may appear narrow during the summer, broader if an annual cycle is considered, and very large if a flood of a century and its effects are included. Many other, including spatial, characteristics will change accordingly.

Ecotone physiology

The primary interest in ecotones is motivated by the potential role they play in maintaining and shaping of various ecological process. Forman & Moore (1992) identify several ecotone functions which largely coincide with our diagram (Fig. 1B). They label these functions as conduit, filter or barrier, source, sink, and habitat. We propose to add feedback as a separate category. We summarize the role of ecotones graphically (Fig. 1B). The role of ecotone, or FUNCTION, appears under five headings: What it *does to* ..., what *feedbacks* it has ..., how it *mediates* exchanges ..., and how it *isolates* .... We differ here from Naiman *et al.* (1992) in breaking the function into more formal yet empirically analyzable components, instead of focussing on epiphenomenological descriptors such as their contribution to stability or to the maintenance of diversity.

What it does to (.. habitats). An ecotone may be a net source of material and energy in form of organisms, structural components such as logs, nutrients, plant carbohydrates, insect proteins, and many others or it may be a net sink. In addition to export and import inherently linked with the sink/source concept (Forman & Moore, 1992), an ecotone modifies habitat of interest. It may modify wind (wave energy, thermal regime), light conditions, or hydraulics (e.g., Bott, 1983).

Feedback. Ecotone may provide a feedback. The contrast between the feedback and sink/source concept is that a feedback amplifies or reduces the intensity of system processes without necessarily being a net sink or source itself. Feedback may occur whenever ecotone and one or both adjacent habitats are interacting synergistically in augmenting, reducing, or maintaining some ecological process. Most likely feedback operates in combination with sink or source process, at least in some dimensions. For example, carp foraging among cattails in a coastal wetland of Lake Ontario (Cootes Paradise) create local passages and open water patches among emergent plants. The created heterogeneity may, in turn, enhance survival and growth of carp fry and juveniles and thus close the feedback loop (see also the paper by Kolasa & Weber, 1994). An ecotone may have multiple feedbacks with both habitats it divides, and each of these sets of feedbacks may be entirely different in nature. The same wetland cattail zone may provide nesting and foraging sites for land animals (muskrats, redwinged blackbirds) whose activities contribute in various ways to the pattern of cattail distribution, reproduction, and growth.

How it mediates. Any transition zone is likely to let organisms, matter, or processes through differentially. It filters them. This aspect has been discussed by landscape ecologists in detail with the exception of, perhaps, one important facet. A filter is always associated with a change of frequency. Thus, any phenomenon crossing a boundary imposed by an ecotone changes its temporal scale of operation (Allen & Hoekstra, 1992). This is important because, in land/water ecotones, the filtering operation often means a smoothing of external impacts. For example, a mosaic of flood plain habitats of different duration, characteristics and connectivity may smooth variation in reproductive success of several fish species of the Danube River (cf. the hierarchy of generalized relevant factors is shown in Fig. 2). Finally, an ecotone is a constraint. The constraint can be thought of as a boundary condition, *i.e.*, a quantitative determinant of how much and which exchanges are allowed across an ecotone. By contrast to filtering function, the constraint refers to allowable magnitudes of phenomena.

How it isolates. There seems to be more to isolation than just being a simple barrier. An ecotone has two sides and the isolation on these two boundaries may be symmetrical but, more likely, it is not. The isolation may scale differently – an ecotone may be porous to particles/organisms of various sizes. For example, lush riparian vegetation of tropical streams and lakes may be penetrable by large animals only to act as an effective barrier to airborne materials. Indeed, the barrier properties of ecotone will differ depending on whether passive or active processes are involved and whether the barrier itself is homogeneous or heterogeneous (Wiens, 1992).

Habitat. Ecotones are indeed habitats. In order, however, to treat them as equivalent habitats to those they divide, or unite, a conceptual shift to another spatial scale must take place (see Fig. 1A, rightmost panel). By definition, a transition zone between two habitats is not at the same hierarchical level as those habitats. Still, a mechanistic understanding of the functions ecotones

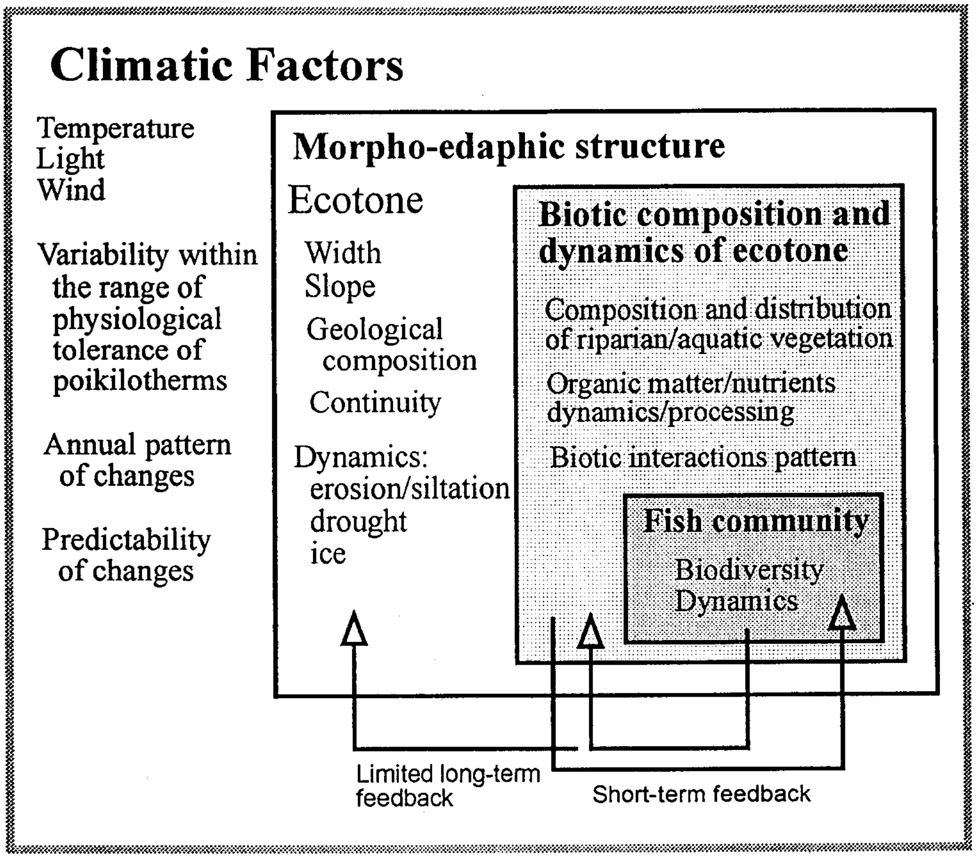

Fig. 2. Hierarchy of factors influencing fish communities in streams – an example of the context and role of ecotones (more explanation in text). Note that suites of factors are associated with different spatial and temporal scales, with nested boxes representing a progressively smaller scale.

provide may still require treating them as independent, self-maintaining entities.

After having reviewed various aspects of ecotone function, we illustrate some of the factors affecting stream fish communities (Fig. 2). We break these factors hierarchically into those that are clearly external and constraining, those that characterize ecotones from the morphological and geological perspective, and those that constitute biotic component, superimposed on and interacting with the former. Figure 2 also illustrates that some of the aspects of the ecotone definition (Fig. 1) fit into different levels of a specific analysis of stream ecotones. For example, 'Aspects to study-composition' belongs to the second innermost box in Fig. 2, while 'Context' appears at the two highest hierarchical levels, *i.e.* Climatic Factors and Morpho-edaphic structure.

Finally, we note that ecotones, being transitional zones, affect various aspects of local ecology. By definition, they change values of many variables such as humidity, temperature, sedimentation rate, and many others. More interestingly, ecotones often accelerate or intensify many processes. Land/lotic ecotones, for example, speed up mineralization of organic matter or accelerate sediment build-up (e.g., Ranwell, 1974). Concentration of energy and nutrients builds often up at ecotones. Lush riparian vegetation and nutrient retention are examples of such processes amply documented for lotic environments.

'Ecotonology' or what is there to study

The study of the role of ecotones ('What it does' component) can be enhanced and deepened by the analysis of the ecotone itself. Such an analysis might include (Fig. 1C) several standard angles or aspects. We group them in four obvious categories of shape, composition, context, and dynamics.

'Shape' may include specific information on the extent, width, sinuosity, continuity, or patchiness of the whole ecotone or one of its edges. By contrast, composition has more than just a spatial dimension. Whenever appropriate, the arrangement of components in space, their frequency and relative sizes, including height, become important attributes to consider. In addition, the biotic (taxonomic or functional) qualities described in terms of guilds, resource base, or impacts on habitat (Fig. 1C) may become subjects of analysis. For example, a stream community shaded by *Eucalyptus* trees may respond differently to CPOM than if trees were willows, maples, or conifers (e.g. Boulton & Boon, 1991). Composition may affect ecotone porosity or permeability to matter and energy fluxes as well as organism movements along the ecotone (conduit; e.g., Forman & Moore, 1992). Another example of the specific impact of composition on the ecotone dynamics is provided by carp (Kolasa & Weber, 1994). Several consequences of composition, spatial arrangements and temporal availability of components within a headwater stream are reviewed in this volume (Schlosser, 1995) and may serve as an example of the complexities involved. Context is yet another important aspect in the study of ecotones. For instance, the same ecotone such a strip of riparian vegetation may play a very different role in a naturally forested landscape from that in an intensely agricultural landscape. The size of the river and the landscape type (contexts) influence the importance of riparian ecotones for fish biomass and communities (Schiemer & Zalewski, 1992). Landscape heterogeneity has a direct impact on fish biomass, productivity and diversity when the landscape becomes a floodplain (e.g. Lowe-McConnell, 1987) and an indirect impact in other situations. Finally, ecotone dynamics is an important but largely neglected aspect. Ecotones do change and the analysis of the rate and conditions under which such changes occur are likely to become an integral part of the understanding of ecotones and their contribution to the maintenance of healthy aquatic ecosystems. In this volume (Kolasa & Weber, 1995) we provide an example of ecotone change and examine some of the possible consequences of this change for community level characteristics.

Conclusions

Understanding ecotones has progressed sufficiently far to justify attempts at a synthetic and general review of ecotone related problems. These problems include clarification of the ecotone concept, enumeration of ecotone roles or functions, and identification of major perspectives within which ecotones require investigation.

The most important aspects identified in this paper are the scale-dependence of ecotones and its significance for making comparisons among ecotones, feedback functions of ecotones, and concentration of ecological processes at ecotones. It appears that the actual expression of ecotone attributes is highly scale dependent. It is thus desirable to give careful consideration to identification of scale, ecotone, and to determination whether ecotone is a boundary *vs* a part of the system before proceeding with field data collection.

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