It is directed more toward the formal structures of natural regions and less toward their functional structures. The most important methodological work in this field in Germany has been done by Paffen (1953). Based on this theoretical work a map of natural areas of Germany with written descriptions of the regions and a long methodological introduction has been created by Meynen and Schmithüsen between 1953 and 1962. Unfortunately this physiognomic approach was lacking essential ecological components including interactions between structures and processes. That is why at the end of the 60s the above mentioned method was supplemented by the taxonomy of natural areas that considers the methodological and practical necessity of quantitative description of regions. Nevertheless it had to deal with the difficulty to include functional ecological variables and processes adequately (see Chapter 6.1).

2.5 Landscape boundaries, ecotones

2.5.1 There is always something between something

Boundaries are everywhere. The human eye and mind differentiate and compartmentalize the world around us, the environment, into units: Rooms, chairs, trees, and mountains. If you have a discrete object, there has to be an end and a beginning to it, its boundary. The skin is the boundary for our bodies for example. It seems a two dimensional surface, but when we start changing scale, like use a microscope, the two dimensions dissolve into a space with three dimensions: hairs, pores, parts of skin etc. Two **fundamental concepts** of boundaries emerge:

- every boundary is in reality a boundary space, a three-dimensional body with boundaries of its own, and
- boundaries are scale- and observer-dependent.

For some microbes, our skin is the environment they live in, for us the skin is the transition to our environment. The necessity for formulating boundaries derives itself partly from the "hierarchy principle" (Blumenstein et al. 2000, see also Chapter 2.4). But those boundaries are analytical in nature and in reality divide a continuous universe. Nevertheless it is practical to delineate subsystems within our universe, simply because our imagination is not able to handle such complexity. The well-known parable of the watchmakers (Simon 1962 in Wu 1999) explains heuristically the need for using systems, subsystems and therefore the boundary concept: Two watchmakers, Hora and Tempus, were making equally fine watches, each consisting of 1,000 parts. Both were frequently interrupted by customers' phone calls, at which time they had to stop working, thus the unfinished watch at hand fell apart. Hora took the hierarchical approach by having his watch built with modules that were further composed by submodules, while Tempus assembled his watch directly from the parts. Eventually, Hora became a rich man, but Tempus went bankrupt. Simple probability calculations reveal that, suppose the probability of an interruption occurring while a part is being added to an assembly is 0.01. Hora makes 111 times as many complete assemblies per watch as Tempus.

If we use this boundary concept in landscape studies, we arrive at the concept of the **ecotone**. Ecotones divide units (homogeneous areas in the scale they are observed), they are often shown as a line on a map, e.g. the coastline on a globe. Clements (in Hansen et al. 1992) first mentioned the term "ecotone" in 1905. He observed that boundary zones between plant communities could combine characteristics of both adjacent communities as well as generate individual features of the transition zone. The roots of the term are Greek, "oikos" meaning household and "tonos" meaning tension. Until the emergence of the "patch dynamics theory", however, the term "ecotone" was unused. It became evident only recently, that ecotones in their function as transition zones actually define patches in the landscape.

A widely accepted **definition of** the term **ecotone** is as follows (Holland 1988): "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."

Keeping in mind that an ecotone can vary in size and in ecological functioning it can be expressed in other terms as: "Ecotones can be viewed as zones where spatial or temporal rates of change in ecological structure or function are rapid relative to rates across the landscape as a whole" (Hansen et al. 1992).

Boundaries can be smooth or sharp, curvilinear or straight (Forman 1995). Straight boundaries and edges are mostly related to human activities and are likely to be anthropogenic. Modern agriculture and infrastructure tends to create straight and sharp linear boundaries. Curvilinear boundaries are more organic and often related to natural landscape elements, such as rivers. Most boundaries show spatial arrangements at different scales. They are organized in different fractal dimensions (Figure 2.5-1).

Van Leeuwen (1970) defined the **extremes of boundaries** as "limes convergens" (sharp edge) and "limes divergens" (smooth gradient). Although being addressed initially to plant communities, these terms were adapted to landscape elements of higher levels of organization. Perhaps due to the decline of Latin language in natural sciences, the terms ecocline (for "limes divergens") and ecotone (for "limes convergens") became more successful.

Initially, these terms were introduced by Westhoff (1974) to describe limits of plant communities.

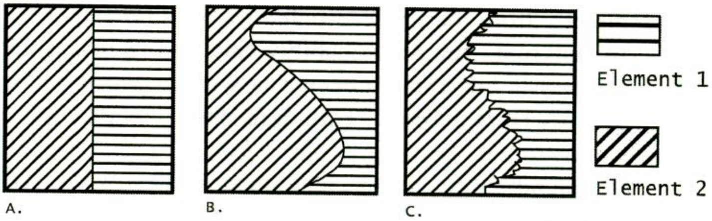

Figure 2.5-1: In landscapes different types of boundaries exist showing variability at different fractal dimensions. This is reflected in straight (A), curvilinear (B) or modified at multiple fractal dimensions (C) (draft: C. Beierkuhnlein)

Van der Maarel (1976, 1990) suggested that a gradual transition should be called "**ecocline**", while the term "ecotone" should be reserved for a sharp transition, an all-or-nothing scenario (see Chapter 2.3.2). So far, some studies have tested this theoretical concept (e.g. Backeus 1993), but the general definition of ecotone as mentioned above in conjunction with the scale dependency seem to have lead to the usage of ecotone for both scenarios. To clarify the concept of ecotones in relation to other concepts in ecology, Hansen and Di Castri (1992) differentiated the several terms (Table 2.5-1).

Table 2.5-1: Terminology for change in space and time

change in space	gradual	ecocline
	abrupt	ecotone
change in time	progressive	ecological succession
	sudden, nonlinear, chaotic	ecotone

2.5.2 Ecotones in theory

Figure 2.5-2 shows four ecosystems and their journey through time and space. Each ecosystem can be perceived as a ball rolling along its trajectory towards an unknown attractor. It has its particular place on the earth's surface (or ocean depth for that matter). Each ecosystem is controlled by different factors, their interactions as well as their changes through time. These are called "controlling factors" (Haken and Wunderlin 1991). In Figure 2.5-2, the array of controlling factors is symbolized by jacks, lifting the space/time continuum, providing possible trajectories and ultimately "channeling" each ecosystem on its way through time and space.

Ecosystem I is running up on a threshold in time, the controlling factors no longer support this particular ecosystem on that particular spot in space.

We could imagine a warming climate in northern latitudes leading to an invasion of tundra by trees. The ecosystem I, arctic tundra, is slowly replaced by another type of ecosystem, let's say boreal forest, ecosystem II. The arctic tundra, before a stable ecosystem on our space-time surface and therefore symbolized as a ball, is entering a **temporal ecotone** stage. The controlling factors no longer allow the existence of pure arctic tundra on this spot. In terms of general systems theory, the arctic tundra is moving through the stage of "critical slowing down" towards instability. This instability is symbolized by the ridge, the "threshold in time". From there, chance and the new controlling parameters will determine which new system will establish itself and where it is moving. This newly established system is truly unique and unparalleled. It might to a wide degree be nearly similar to ecosystems we can encounter in other places on the earth. But with a look on the time-space continuum, we can see that this point/ecosystem in time has its special and unique history. To what degree the history of this point will impact the future can only be guessed.

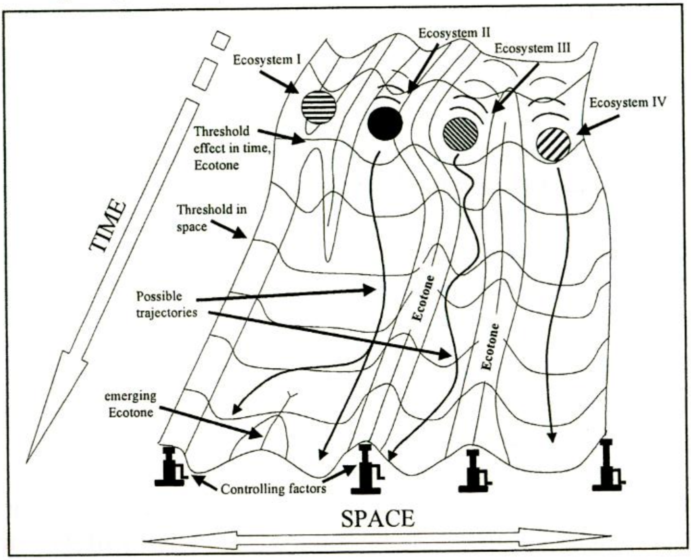

Figure 2.5-2: Four ecosystems on their journey through time and space. They are following their trajectories, guided by an energetic "landscape". Controlling factors are symbolized by jacks, lifting the time-space continuum, creating the conditions in which ecosystems and their ecotones evolve, exist and perish

Let us now focus our attention on ecosystem II. It is confined by an array of controlling parameters or environmental factors. They are symbolized by the ridges between ecosystem II and ecosystems I and III. These ridges are transition zones between two adjacent ecosystems, ecotones. They are themselves unstable and need input (energy, matter, information) from both sides/ecosystems to exist. As we can see, time changes the position of the **ecotone in space**. To stick with our image from the beginning, we could imagine shifting biomes due to climate change. The ecotones or transition zones between them shift accordingly.

As ecosystem II moves along its trajectory, it encounters a rising ridge, an emerging control parameter. As example we could think of the control parameter "human land use". Ecosystem II can no longer exist where additional energy input through intensive agriculture changes the environmental variables. The new and emerging ecotone might be the transition zone between forest and fields.

Ecosystems III and IV are moving along their trajectories, uninterrupted by unexpected, chaotic events or strange attractors. Ecosystem III might be recovering from a disturbance, staggering along. The curvy trajectory symbolizes resilience. The system is pushed and reacts with sideways motion, but does not go "over the edge". It remains stable in its setting.

2.5.3 Ecotones in reality

The recognition of a transition zone between two ecological systems by Clements (1905, in Hansen et al. 1992) could be called the beginning of ecotone research. Obviously the recognition focussed on the spatial aspect of ecological systems and their boundaries within a given area. Later on, after development of the theoretical foundations (which is still ongoing), the concept was used not only in spatial but also temporal terms (e.g. Delcourt and Delcourt 1992). Keeping in mind that every boundary and its classification is scale dependent, we can identify ecotones where

- a steep environmental gradient exists, that directly affects ecosystem function, structure and composition. Example: Boundary between forest and fields in anthropogenic landscapes, and
- nonlinear response to a gradual change of environmental variables is found, the "threshold effect" or the effect of cumulative impact. For example a pH change below 5.5 in the soil leads to mobility of Al^{3+} -ions with toxic effects on many plants as well as to ground water contamination (Blume 1990).

Ecotones as the boundaries between different ecological systems can emerge on a variety of **scales**. Just as the ecosystem itself can vary in spatial extent as well as occupy different levels in the spatial hierarchy (see Chapter 2.4), its boundaries, the ecotones can be found on different hierarchical levels. Gosz (1993) proposed an "ecotone hierarchy" ranging from the biome ecotone (the biome transition area) to the plant ecotone (Table 2.5-2). Examples of studies covering the whole range of scales in ecotone research are

Bretschko (1995), Kieft et al. (1998), Neilson (1993). The hierarchy is closely linked to probable constraints or controlling factors, which at the biome level are macroclimate and its variation through major topographic structure (Figure 2.5-3). The finer the scale and therefore the hierarchical level of the ecotone, the more controlling factors influence the ecotone. In addition to the number of controlling factors, their kind and type change with each hierarchical level. At the lower end of the hierarchy, the **plant ecotone** level, macroclimate and the major topography are constant, but the differentiation between different ecotones is rather controlled by factors such as microclimate, soil fauna, soil hydrologic regime etc. At increased finer scales the possible combination of controlling factors is much higher than at the coarser levels, simply because it is influenced by all factors above it in the hierarchy! The **biome ecotone** (a large scale phenomenon) may be a result of two or three controlling factors (in our perspective). The **landscape ecotone**, however, is already influenced by the biome it is located in, therefore by its controlling factors, PLUS additional factors on the landscape level. Macroclimate and topography are influencing the landscape ecotone as well as e.g. soil distribution, geomorphic structure and mesoclimate.

Table 2.5-2: Ecotone hierarchy, based on Gosz (1993)

	ecotone hierarchy focussed on ecology	proposed hierarchy focussed on integral ecological landscape units	controlling factors (each ecotone is influenced by controlling factors of its own level and in addition by every controlling factor above its level)
macro scale		land-ocean ecotone (global)	distribution of continents on earth surface
	biome ecotone	ecozonal ecotones	macroclimate, major topography
mesoscale	landscape ecotone	landscape ecotone	mesoclimate, geomorphic processes, soil characteristics
	patch ecotone	top ecotones	microclimate, microtopography, soil/soil moisture variation, species interactions
microscale	population ecotone, plant pattern		interspecies interactions, intraspecies interactions, physiological controls, population genetics
	plant ecotone		soil fauna, soil flora, soil chemistry

The highly differentiated site conditions of ecotones cause special combinations of species and communities, a high richness in species is usual (see Chapter 2.8.5), but ecotones can also display less biodiversity than the neighboring ecosystems (Neilson et al. 1992). But ecotones often act as **barriers** in ecosystems (Blumenstein et al. 2000). They are always areas of discontinuity. This discontinuity explains in part the emergence of structure as part of feedback loops. Once a boundary is manifested, gradients will control the flow of energy, matter and information across it. The different strength of gradients leads to increased differences in the two systems bounding the gradient. In the soil for example, differences in the redox potential of a water saturated sediment layer can lead to different felling of Fe- and Mn-molecules. This is an important prerequisite for the development of rosty patches and concretions in the oxidized layer of a gleyic soil (Scheffer and Schachtschabel 1992).

Figure 2.5-3: The forest steppe zone in Asia is a broad ecotone between the steppes in the south and the zone of compact forests (taiga) in the north. Due to extreme climatic conditions, and supported by human activities (timber cutting, grazing), in the northern Mongolian mountains mainly northern slopes are covered by forests, while dry southern slopes are dominated by grass and herb steppe ecosystems (Photo: O. Bastian 1994)

The ecotone concept can be applied to both spatial and temporal investigations. If we could directly observe one particular spot on the earth's surface through time, we would always see change under way and never perceive a stable state of this one spot for very long. Through thousands or even millions of years our spot might change from being part of the ocean to a shallow lake to a steppe type ecosystem. We would maybe see a cooling of temperatures, a change in species composition, the advancement of the ice shields, their retreat and the recolonization of our spot starting with gravelly soils, the first lichens arriving, mosses, brushes etc. until we might see a forest. Through some of our observation we could identify an ecosystem in a quasi stable state, meaning that the controlling factors and their "answer by nature", the ecosystem at that time, are in equilibrium. A lot of scientific research has focussed on these "stable states" and only lately has attention been given to the dynamic and change of these systems. These times of increased change, maybe even catastrophic in nature, are ecotones in time.

2.5.4 Delineation of ecotones

Methods for ecotone detection include spatial analysis (GIS and remote sensing, see Chapters 6.2 and 6.3) for the detection of patterns in space (Fortin et al. 2000) and statistical methods applicable to both spatial and temporal datasets. Fortin et al. (2000) also include modeling as detection methods for ecotones by formulating and predicting interactions in multivariate datasets. In general, ecotone detection is the ability to determine spatial or temporal change (Johnson et al. 1992).

Table 2.5-3: Overview of statistical methods available for detection, measurement and characterization of ecotones (from Fortin et al. 2000)

ecotone attribute	data type grid data (raster format, e.g. in GIS)	transect data	sparse data, unevenly distributed
detection	edge detection algorithms and kernels	magnitude of first difference	irregular edge detection
location	thresholding of edge operations	maximum of first difference	functional criteria
width	goodness of fit for location statistics	magnitude of first difference	magnitude of first difference
evenness	dispersion of width along boundary		dispersion of width along boundary
sinuosity or Curvilinearity	length of boundary as a function of grid precision; fractal dimension		length of boundary as a function of grid precision; fractal dimension
coherence and significance	boundary statistics overlap statistics (different between boundaries in vegetation, soil, etc.)	coincidence of limits more often than by random chance	boundary statistics overlap statistics (different between boundaries in vegetation, soil, etc.)

For an overview of statistical methods concerning detection of patches in landscapes and therefore ecotones as their boundaries see Fortin et al. (2000), Johnston et al. (1992) and Turner et al. (1991). Some detection mechanisms include: GIS functions (e.g. pattern recognition, optimal corridor location, fractal dimension), "moving (split) window" technique, especially suited for transect data, "wombling" (lattice, triangulation, categorical), essentially a two dimensional form of the moving split-window technique. Once ecotones are detected they can be measured for width, verticality, evenness and curvilinearity (total length divided by straight line length) or sinuosity (length of ecotone per unit area using fractal dimension, Table 2.5-3).

2.5.5 Ecotones and change

Ecotones are often described as "early warning stations" for a change in structure and composition of the adjacent ecosystems (Allen and Breashears 1998). Meaning that if controlling factors are changing (e.g. mean annual temperature increases under global warming scenarios), the change and effects of that change can first be detected in the boundary zone, the ecotone. This is based on the assumption that the limiting factor delineating the spatial extend of that ecosystem at that time continues to be the limiting factor after the change took place. This is not always the case and studies not supporting this view are documented (Neilson 1993).

Let us look at one example, the **treeline-ecotone in interior Alaska:** During the last decades, the Arctic and Subarctic are experiencing warmer temperatures both in summer and winter (Juday et al. 1998) and global change is heavily impacting high latitude ecosystems. One of the most visible natural ecotones is the treeline-ecotone, dividing in our case the boreal forests and the arctic or alpine tundra. Fundamental interest in the question of possible treeline movement under global change is fueled by the question of carbon uptake of the boreal forest ("sink-source question"), albedo changes and other feedback loops between boreal forest and global climate (Foley et al. 1994). This treeline is generally thought to be correlated with the July 10°C isotherm (Daubenmire 1954). The limiting factor for tree growth is therefore believed to be temperature. Under global change scenarios, the vegetation zones will eventually adapt to higher mean annual temperatures and changes summer and winter conditions (Chapin et al. 1995). This logical reasoning is based on the assumption that temperature will still be the limiting factor for tree growth under changed conditions. However, new findings suggest, that the limiting factor for tree growth and establishment may have shifted to moisture supply within the boreal forest and at least parts of the forest-tundra ecotone in Alaska (Jacoby and D'Arrigo 1995). Briffa et al. (1998) reported a decreased sensitivity of radial growth of high latitude trees to temperature since the mid 20th century. This would have a major impact on the forest-tundra distribution in interior Alaska. Two scenarios are most likely:

1. The forest will expand into tundra with increased summer air temperatures, providing a higher CO_2 uptake and a negative feedback to the greenhouse effect (our "limiting factor stays the same scenario")

2. Under increased summer air temperatures the limiting factor of tree growth will shift to moisture supply, possibly leading the ecosystem trajectory towards higher fire frequency, massive die-back of white spruce due to moisture stress and slow change into aspen parkland, resulting in another positive feedback loop with less CO_2 uptake and increased greenhouse effect.

These scenarios make clear that completely different outcomes are possible due to a small change in the ecosystem trajectory. There is no real way of sure prediction. Predictions based on linear causal chains might just be lucky hits, if nothing fundamentally changes within the ecosystems in question. As outlined above, this is not always (actually seldom, Briggs and Peat 1993) the case. Under these more realistic circumstances we will be able to use a ton of colorful prediction maps as wallpaper in storage rooms. Going back to Figure 2.5-2 we can now ask, if the boreal forest ecosystem faces the destiny of ecosystem I, running against a threshold in time and subjected to fundamental changes in internal structure, or ecosystem III, shaken, but still on its way through time, adapting by spatial change and shifts in biome location.

As a careful first **conclusion** we might say that:

- Small and slow shifts in controlling factors lead to a gradual spatial shift of the ecosystems involved as long as the limiting factor is not changing. The change can be first detected in the ecotone areas.
- Catastrophic events, nonlinear responses and change in limiting factor can lead to different ecosystem trajectories, change is not first detected in the ecotones.
- If the monitoring interest is focussed on ecotones in time, the core areas of biomes might provide a more suitable homogeneous background for detection of change, e.g. regional drought-stress (Neilson 1993).

2.6 The catena principle

Experience of surveying natural units in hilly areas has shown that certain ecotopes regularly recur within certain natural areas on the chore scale. Although working separately, both Haase (1964) and Klink (1964, 1966) introduced the term "ecological catena" for such regular sequences of ecotopes during their studies in the hills of Lusatia and in the highlands of Lower Saxony, respectively. The term is actually an extension of the catena concept coined by Milne (1935) and Vageler (1955) in mapping tropical soil series. Such ecological catenas were termed "Standortsketten" (**site chains,** Kopp 1961) in forestry mapping, and Standortsreihen ("site series", e.g. Schmithüsen 1968) in vegetation geography.