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Submitted to *Environmental Management* 6/30/03; revised 11/11/03; accepted 11/15/03

Identifying Ecoregion Boundaries

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ABSTRACT

This article summarizes the rationale I used in identifying ecoregion boundaries on maps of the United States, North America, and the world's continents, published from 1976 to 1998. The geographic reasoning used in drawing boundaries involves 20 principles, which are presented to stimulate discussion and further understanding. Brief background and references are provided for the principles.

KEY WORDS: Ecosystem geography, ecoregions, mapping, boundaries, United States, North America, world

Ecoregion maps show the Earth's surface subdivided into identifiable areas based on macroscale patterns of ecosystems—that is areas within which there are associations of interacting biotic and abiotic features. These ecoregions delimit large areas within which local ecosystems recur more or less throughout the ecoregion in a predictable fashion on similar sites. For example, trees that respond to additional moisture on north-facing slopes are seen repeatedly throughout the semi-arid and arid regions of the American West. In many areas natural ecosystems have been profoundly modified (e.g., land clearance or fire) or replaced by introduced plants and animals. To discern patterns in such areas, the nature and causes of the spatial patterns that would have existed in the absence of disturbance are considered.

Groups of spatially related ecosystems can be considered an ecosystem of higher order and commonly greater size, which I have proposed to call "macroecosystem." This terminology extends from the classical use of the term "ecosystem" as proposed by Tansley (1935), in which the latter term is applied only to the smallest units. The natural patterns and processes of a particular ecoregion provide essential keys to the sustainability of ecosystems and can inspire designs for buildings and landscapes that sustain themselves (Bailey 2002). Because of this, they have been widely applied in conservation and management programs. For example, in 1993, as part of the National Hierarchical Framework of Ecological Units (Cleland and others 1997), the U.S. Forest Service adopted ecoregions for use in ecosystem management.

The term "ecoregion" was first proposed in 1962 by the Canadian forest researcher Orie Loucks (1962). In 1967 Crowley (1967) mapped the ecoregions of Canada based on macro features of the climate and vegetation. Following Crowley's concepts, I mapped the ecoregions of the United States (1976, revised 1994), North America (1981, revised 1997), and the world's continents (1989) and oceans (1996). A simplified, reduced-scale version of the continental map appears in my books, *Ecosystem Geography* (1996) and *Ecoregions* (1998a), and the 20th edition of *Goode's World Atlas* (Hudson and Espenshade 2000). I described the units shown on the maps and explained how and why they are distributed in a number of publications (Bailey 1983, 1989, 1995, 1996, 1998a, 1998b; Bailey and Hogg 1986). These publications briefly discuss various aspects of how ecoregion boundaries are set. Others have prepared maps depicting ecoregions of large areas, including the U.S. Environmental Protection Agency (Omernik 1987), the Sierra Club (Elder 1994), The Nature Conservancy (1997), the Commission for Environmental Cooperation (1997), the World Wildlife Fund (Olson and Dinerstein 1998), and the Food and Agriculture Organization of the United Nations (FAO 2001). Ecoregions have been mapped and described for some states (cf., Nowacki and others 2002, Nigh and Schroeder 2002, Albert 1995). Recently, federal natural resource agencies in the United States have worked to develop a map of common ecological regions (McMahon and others 2001). The geographic distribution of ecoregions is correlated in varying degrees with large homogeneous units of biota such as life zones (Merriam 1898), bioregions (Van Newkirk 1975), biotic provinces (Dice 1943), biogeographic provinces (Udvardy 1975), biomes (Clements and Shelford 1939), zonobiomes Walter (1985), and life-place (Thayer 2003). Others have drawn a connection between ecoregions and environmental regions that are built to address social, economic, and environmental issues of a particular place (Foster 2002).

Invariably the question arises, “What are the differences between these maps?” The objectives of this article are to summarize the rationale I have used in identifying terrestrial ecoregion boundaries, clarify my approach, and indicate the problems. The primary problem is the necessity of synthesizing a variety of clues (climate, physiography, physiognomy of the vegetation, ecotonal changes, and so on) in order to arrive at reasonable boundary placement. The product of this ecological synthesis has limitations that I will address later. I expect that this article will stimulate discussion and enhance understanding of ecoregion concepts.

Geographic Reasoning in Identifying Ecoregion Boundaries

Ecoregions naturally often exist in different sizes and can be identified at various scales or levels of detail in a hierarchical manner. A hierarchy of boundaries allows the incremental viewing of the world’s environment from a very broad perspective or varying degrees of resolution. While the concept of ecosystem implies equality of level among all the components of the system, all those components are not equally significant in defining levels in the hierarchy (Bailey 1985, 1988a, 1996, Klijn and Udo de Haes 1994).

Climate largely determines natural ecosystem boundaries of all scales (cf., Holdridge 1947, Walter 1985, Schmidt 1979, Ecoregions Working Group 1989, Neilson 1987, Schultz 1995, Bailey 1996). The basic assumption here is that climate, as a source of energy and moisture, acts as the primary control for the ecosystem. As this component changes, the other components change in response. Climate, in turn, is channeled, shaped, and transformed by the structural characteristics of the ecosystem, that is, by the nature of the Earth’s surface. In this sense, then, all ecosystems, macro and micro, are responding to climatic influences at different scales. This approach solves the problem with using other components that are subject to rapid change, such as biota. It will screen out the effects of disturbance and succession, permitting identification regardless of what biota currently exists. For example, a given area may be supporting forest, or recently disturbed open lands, depending on disturbance events, yet this area still represents the same ecosystem. Present vegetation is useful for describing the status of the ecosystem in terms of age or disturbance, not to delineate the boundary of the system.

The most important climatic factor is the climatic regime, defined as the daily and seasonal fluxes of energy and moisture (Troll 1966). As these change, the kinds and patterns of dominant life forms of plants and animals change, as do the kinds of soils. For example, tropical rainforests have latosolic soils and are associated with hot and wet climates. Climate changes invariably alter hydrologic and erosion cycles plus life cycles of the biota. All this implicates climate as the most important factor to consider in setting ecoregion boundaries. It follows that ecoregions should reflect significant differences in climate. From my three decades working to capture and depict climate-based ecoregions the world over, and from observing what others have written about the subject, I have discerned the following principles:

1. *The series of ecoregions should express the changing nature of the climate over large areas.* Unfortunately, climate varies within short distances owing to variations in local landform features and the vegetation that develops on them. It is necessary, therefore, to postulate a climate that hierarchically lies just above the local modifying irregularities of landform and vegetation. To this climate the

term “macroclimate” is applied. Macroclimates are among the most significant factors affecting the distribution of life on Earth. As the macroclimate changes, the other components of the ecosystem change in response. Macroclimates control the distribution of plant formations (cf., Box 1981), influence soil development, help shape surface topography, and affect the suitability of a given system for human habitation. As a result, ecosystems of different macroclimates differ significantly. Because meteorological stations are absent or sparse in many areas, data are simply not available to map precisely the distribution of these ecological climates. Thus, we substitute other distribution-bases, such as vegetation, that are the visible and tangible expressions of climate. Generally, each climate is associated with a single plant formation class (such as broadleaf deciduous forest), characterized by a broad uniformity both in appearance and in composition of the dominant plant species. Of course, not nearly all the space is taken up by the formation, for the nature of the topography will allow the differentiation into many habitats, and the percentage of the region occupied by the ecosystem that characterizes the formation will depend upon the amount of well-drained upland. Steep slopes that are hotter and dryer or cooler and moister, as well as bottomlands where water lies near the surface will be occupied by other ecosystems. An ecosystem that broadly conforms to macroclimate is termed *zonal*. Local ecosystems correlate with many of the variations from the zonal pattern. The term *azonal* is applied to these variations. Damman (1979) gives other vegetation criteria that can be used to recognize regional differences in climate.

2. *Boundaries of ecoregions coincide with certain climatic parameters.* For example, the boreal zone is a climatically determined ecological unit dominated by coniferous forest. The zone's poleward limit corresponds roughly with the isotherm for the mean daily temperature of the warmest month that is too cold for tree growth. Similar constraints apply to the equatorward limits of the zone. For example, the southern boundary roughly approximates the line along which the mean daily temperature is warm enough to allow other kinds of trees. This is where the deciduous broadleaf forests of the mid-latitude zone begin. However, temperature alone as a basis of ecoregion delineation is unsatisfactory because humid and arid regions receive no distinction. The boundary between the boreal zone and the mid-latitude grasslands in Siberia and the Canadian prairie areas is controlled by the dryness of the climate rather than by its temperature. Based on macroclimatic conditions and on the prevailing plant formations determined by those conditions, I subdivided the continents into ecoregions with three levels of detail. Of these the broadest, *domains*, and within them *divisions,* are based largely on the broad ecological climate zones of the German geographer Wladimir Köppen (1931; as modified by Trewartha 1968). It is a system based on quantitative definitions and as such can be applied to any part of Earth where climatic data are available. The definitions and boundaries are presented in **Table 1**. Thermal and moisture limits for plant growth and distribution determine the class boundaries chosen. For example, in Eurasia and North America trees generally cannot grow beyond about 70° N latitude because it has a summerless

climate. In this climate no month has a mean monthly temperature higher than 10^{o}C, which closely coincides with the northernmost limit of tree growth; hence it separates the regions of boreal forest from treeless tundra. Domains are groups of related climates. There are four groups. Three are humid, thermally differentiated: polar, with no warm season; humid temperate, rainy with mild to severe winters; humid tropical, rainy with no winter. The fourth, dry, is defined on the basis of moisture alone, and transects the otherwise humid domains. Within these groups 15 climate types show seasonality of precipitation, degree of dryness, or a degree of cold. For example, within the humid tropical domain rainforests with year-round precipitation can be distinguished from savannas with winter drought. Although climatic parameters were used to establish ecoregional differences, no attempt was made to use the parameters (temperature and precipitation) to establish boundaries. Instead, climatic differences were inferred where discontinuities appeared in physiography and/or vegetation physiognomy. This is a process climatologists use to extrapolate their point measurements.

3. *Fine-scale climatic variations can be used to delineate smaller ecological regions.* The climate is not completely uniform with climatic divisions, so further subdivision can be undertaken. Local contrasts break up and differentiate the major, subcontinental zones. Within the arid zone, for example, deserts that receive only winter rain (Sonoran Desert) can be distinguished from those that receive only summer rain (Chihuahuan Desert). The vegetation of the savanna zone is highly differentiated. Heavy forests characterize its boundary with the

equatorial zone and sparse shrubs and grasses distinguish its arid border. Homer Shantz (in James 1959) recognizes three woodland savanna types in the transition zone between the selva of the Congo and xerophytic shrub of the Sahara that are related to variation in length of the dry season. We refer to these as climate subtypes. The subtypes largely correspond to major plant formations, which are delimited by growth form of the dominant vegetation. They form the basis for subdividing ecoregion divisions into *provinces*. In the south, bordering the selva, the first subtype is formed by the high grass-low tree savanna, composed of grasses that, at maturity, reach heights of three or four meters, mixed with a fairly close scattering of low trees. Farther north, in the direction of decreasing rainfall, this formation gives way to the acacia-tall grass savanna, composed of grasses growing from one to one and a half meters tall and associated with scattered, flat-topped acacias which stand farther apart than the low trees of the southernmost subtype. Still farther north is the acacia-desert grass savanna, where the stunted trees stand far apart and the short desert grasses cover most of the surface. Another example of local contrasts within a major zone is provided by Canadian geographer Kenneth Hare (1950) who recognized three subzones within the boreal zone of the northern hemisphere: closed-crown forest, woodland, forest-tundra.

4. *Boundaries should capture the effect of mountains on climate.* The arrangement of the ecological climate zones depends largely on latitude and continental position. This pattern, however, is overlain by mountain ranges, which cut across

latitudinally oriented climate zones to create their own ecosystems. Elevation creates characteristic ecological zones that are variations of the lowland climate. Mountains show typical climatic characteristics, depending on their location in the overall pattern of global climatic zones. The mountain ranges of Central America, for example, experience the same year-round, high-energy input, and seasonal moisture regime consisting of relatively dry winter and rainy summer typical of their neighboring lowlands.

5. *A uniform pattern of mountain zonation is repeated over a climatic zone, which is the basic element in regionalizing mountainous territories.* Where groups of ecosystems cover large areas, in a quasi-uniform way, their mapping presents little difficulty; but simplifying and generalizing mountainous ecosystems into ecoregions presents a more difficult problem. A suitable solution is to consider the sequence of elevational belts. Between the individual elevational belts, a lively exchange of materials occurs: water and the products of erosion move down the mountains; updrafts and downdrafts carry dust and organic matter; animals move easily from one belt into the next; and wind and birds spread pollen and seeds (Walter and Box 1976). The belts, as a result, are interconnected and the geographic area over which a sequence of belts extends is considered to be a large ecological unit, an ecoregion. In this sense, we do not treat the montane forest belt as a separate ecoclimatic zone but rather as only one member of the total sequence of elevation belts. Montane belts in the mountainous areas of different climatic zones are just as distinct from one another as the montane belt is from

other elevation belts in the same zone. These units correlate with the distribution of the lowland climatic zone within which the mountain range is located. Every mountain within a climatic zone has a typical sequence of elevational belts: generally known as montane, alpine, and nival; but those exhibit considerable differences according to the zone where they occur. When a mountain extends over two or more climatic zones, it produces different vertical zonation patterns. Thus, for instance, in the semiarid portion of the Rocky Mountains in the United States, the lowermost zone is a dry steppe, above which lies a lower montane zone (also referred to as subalpine) of dry pine forest, an upper montane zone of fir and spruce, then alpine tundra, and finally perennial ice and snow. In the Canadian Rockies, which are located in the boreal zone, the montane coniferous belt appears as lodgepole pine and spruce-fir forest as the lowermost zone, followed above by tundra and ice. Ecoregion boundaries are set where the vertical zonation patterns change. Such mountainous environments are termed *mountain provinces*.

6. *Ecoregional boundaries should delineate groups of upland sites with similar characteristics.* Landform (with its geologic substrate, its surface slope, and relief) modifies macroclimate to local climate, or topoclimate. Sites to be considered in ecoregional delineation should be reasonably uniform sets of uplands with well-drained surface, moderate surface-slope, and well-developed soils. In this manner the effects of landform differences are screened out, leaving the biologically effective climate as the main variable between ecoregions. These

sites correlate with *zonal* sets of ecosystems; the others are azonal (see 1, above). In highly diversified terrain, zonal ecosystems may occupy only a small fraction of the total area. Azonal systems are associated with unstable sites, such as steep slopes and floodplains.

7. *The mosaic of ecosystems found in major transitional zones (ecotones) should be delineated as separate ecoregions.* These are areas in which two types of plant formations grow side-by-side under the same macroclimatic conditions. The relief-induced topoclimate and/or soil type determines the appearance of one or the other type. The transition zone begins at that point where one vegetation type appears as extrazonal islands dispersed throughout another vegetation type. The islands become larger and flow together, until finally the second type prevails and the first is represented only as islands. These islands become smaller and finally disappear completely; at which point the ecological zone of the second type begins. The boundaries between adjacent ecoregions of this type are usually difficult to locate precisely. Frequently, one ecoregion merges gradually into another. Any line separating the two must then be drawn more or less arbitrarily. A convenient way of roughly fixing the boundary between two adjacent regions is to draw the line where the dominant plant formations of the two regions cover approximately equal area. A good example is the forest-tundra subtype of circumpolar regions in the northern hemisphere, a mixture of tundra on the drier ridges and woodlands in the valleys. This area is a classic example of an ecotone where two major zones, the tundra and the boreal, interpenetrate and blend into

each other (Hustich 1953). Other examples of these types of ecotonal regions are the prairie parklands (N. America, **Figure 1**) or birch-aspen forests (W. Siberia).

8. *Context is often as important as content in mapping ecological regions, depending on scale.* A meadow surrounded by a forest, for example, while similar to a large expanse of grassland, behaves differently because the adjacent forest influences it. The forest affects the microclimate and the plant cover of the meadow, sheltering the meadow from drying winds or from hail. Many bird species that nest in the forest feed in the meadow, and meadow rodents like to hibernate at the edge of the forest or in its interior, so it should be considered part of the climatic forest ecoregion. Likewise, individual lowland basins in the Great Basin of Nevada that are surrounded by widely spaced mountain ranges should be considered part of a single ecological unit that consists of both the mountains and the basins. As water from the mountains flows to the basins, and as the mountains affect the climate of the basins through sheltering, two large-scale linkages are evident. Such linkages create real economic and ecologic units. Another example is where mountains or plateaus meet plains. In many cases the orographic (meaning “related to mountains”) and vegetation boundaries do not always coincide. For example, the vegetation of the plains commonly does not stop at the foot of the mountain but extends up the lower slopes and valleys that drain the mountain. In this case, the orographic boundary is the one that is used to separate the ecoregions—the vegetation of the plains that occurs on the mountain slope or up the valley is considered part of the sequence of elevation. The

grouping of ecosystems to define ecoregions is analogous to using combinations of soils in defining soil catenas (associations) or landforms in defining watershed basins. However, ecosystems related by geography are not necessarily related by taxonomic properties. The catena, for example, comprises different taxonomic soils series that are geographically related. In hierarchy theory these systems are inserted, or nested, into each other (Allen and Hoekstra 1992). The higher level constitutes the environment of the system at the level below it and therefore conditions or controls the behavior of that lower system.

9. *Because subsystems can be understood only within the context of the whole, a classification of ecoregions begins with the largest units and successively subdivides them.* Ecological land classification (which includes ecosystem regionalization) is a deductive process, dissecting wholes into parts on the basis of differences so that classes and units are arrived at by subdivision “from above.” The reason for this, as Rowe (1979) explains, is that classification “from below” cannot discover significant ecological units. They must be apprehended as wholes that have some processes significance. For example, a floodplain is a pattern of spatially associated but *unlike* land units. The floodplain consists of the active channel, abandoned channel, islands, lakes, wetlands, terraces, and so forth. Each unit has different characteristics but is united with the others by common process of development, namely cyclic inundation, erosion, meandering, and deposition. Classification from below by aggregating units will never arrive at the unit “floodplain,” for it is an illogical pattern of spatially associated

components. The unit known as a floodplain only comes into existence through the understanding of a significant formative (genetic) process (see 15, below). In this case a mix of local ecosystems or land units is repeated over the land forming a landscape, which is the basic element in an ecoregion at the next broader scale. Understanding the processes of ecosystem differentiation is essential to identifying ecoregions as well as landscapes such as floodplains. Another problem occurs when ecosystem maps derived from different scales are overlaid in an attempt to identify subsystems (Bailey 1988b). To overlay, for example, the highly generalized boundaries of ecosystems plotted on a regional or global scale onto a pattern of ecosystems plotted in detail almost invariably results in considerable lack of correspondence in boundaries. This is because the maps were derived independently with no whole system in mind.

10. *The factors used to recognize ecoregions should be relatively stable.* The composition of the vegetation of the ecoregion changes with time in a sequence from pioneer vegetation through successional series of intermediate steps to a relatively stable state called late successional vegetation (climax in the sense of Weaver and Clements 1938). The late successional types are used to characterize regions because they tend to be far more site-specific than pioneer types, which may occur over a wider range of conditions. Furthermore, they are used as baselines for contending with the temporal variability associated with disturbance regimes and attending successional states of the vegetation.

11. *Boundaries should circumscribe large, contiguous areas.* The concept of ”ecoregion” differs from that of ”biome,” for a biome is coincident with its climaxes. Every area having the same climax, however far detached from the main area of that climax, seems to belong to the same biome. An ecoregion, in contrast, is never discontinuous (except for marine islands), though ecologic communities somewhat similar to those characteristics of a particular region may exist far beyond its boundaries. I follow Dice (1943) and define each ecoregion as comprising both the climax communities and all the successional stages within its geographical area, and it thus includes the fresh water communities.

12. *Potential vegetation, in contrast to actual, or real, vegetation, is useful in capturing ecological regions.* In some areas problems resulting from disturbance and the occurrence of an intricate pattern of secondary successional stages make regional boundary placement particularly difficult because the patterns of existing vegetation do not correspond well with the patterns of ecoregions (Wright and others 1998). Those problems can be overcome by considering the pattern displayed on maps of potential natural vegetation. For instance, Küchler’s (1970) map of the United States could be used to delineate ecosystem regions if certain amendments are made. Some of Küchler’s mapping units show the presence of large areas of azonal soils, such as sand-plains and salt deposits (**Figure 2**). On the other hand, the same vegetation may exist in different ecoregions due to compensation factors, such as soil, that override the climatic effect. For example, in the High Plains and southwestern United States forests extend into arid and

semiarid regions along streams because of the extra water supply. Ponderosa pine and shrub islands within the grasslands of these regions indicate rocky soil conditions, forming reservoirs of water for taproots. In these cases, a map of ecosystem regions would ignore such areas and relegate edaphically controlled ecosystems to a lower level of classification and more detailed maps. The ecoregion boundaries cannot be compiled from the boundaries of individual ecosystems, however, since the latter are not always easily assigned to either of their neighboring ecoregions; certain types of ecosystems are common to both ecoregions (see *8*, above, **Figure 3**).

13. *An understanding of the relationships between successions on identical landform positions in different climates is useful for establishing meaningful ecological regions.* Slopes of similar physical characteristics will be found in various ecoregions and will support different ecosystems because of the different climates. For example, a certain slope in the arctic will support low-growing shrubs and forbs, whereas an identical slope in a warm continental ecoregion will have dense broadleaf deciduous and needle-leaf evergreen forests. In Ontario, Canada, Angus Hills (1960) and his co-workers (see Burger 1976) defined ecoregions (called “site regions”) within which specific plant successions occur upon specific landform positions. Conversely, similar landforms (topographic form and surficial geology) within different regions will support different plant successions. The different plant succession/landform relationships in various site regions are a reflection of differences in regional climate. **Table 2** demonstrates

how, for the same normal soil moisture condition but with three different topoclimates (normal, hotter than normal and colder than normal) three species of trees (white spruce, sugar maple, and hickory) change their preferred positions in the seven most eastern site regions in Ontario. With these changes related changes also occur in the vigor of other tree species, ecosystem productivity, and type of ground vegetation, which competes with forest regeneration.

14. *Geologic factors may modify zonal boundaries.* Isachenko (1973) described how this works: In uniform geological-geomorphological conditions the transition between adjacent zones is often extremely diffuse; but where the surface is variegated, zonal boundaries assume a more distinct form. The northern boundary of the forest-steppe zone on the Russian plain illustrates the concept. This boundary lies along the interface of two distinct types of geology: one elevated, dissected plains with loess-type carbonate soils, and the other low-lying, sandy forest areas. The former favors the growth of broadleaf forests and the spread of steppe grasslands. The latter, by contrast, favors a southward shift of the tayga's swamps and conifer forests. Accordingly, the boundary between the forest (tayga) and the forest-steppe zones generally lies directly along the interface of such lithologic regions. In the Baltic region, owing to the widespread distribution of carbonate rocks, the northern boundary of the mixed-forest zone is displaced far to the north so that its actual position varies with the theoretical position. In fact, the zonal boundary would lie much further south if we used the

zonal-climatic criteria. Kruckeberg (2002) gives additional examples of this process.

15. *Establishing a specific hierarchy of ecoregional boundaries should be based on understanding the formative processes that operate to differentiate ecoregions at various scales.* Just as full understanding of an organ in the human body or a town requires information from both broader and finer scales, understanding an ecoregion requires information on the broader ecoregion that contains it and on the finer-scale local ecosystems. Two primary sources of energy and their resultant processes differentiate the Earth's surface into ecosystems; one is external, provided by the sun. The sun's energy interacts with the atmosphere to create climates. The factors controlling spatial variation in climate (and therefore ecosystems) are at several levels. At the global level ecosystem patterns are controlled, or caused, by variation in macroclimate related to variation in the solar radiation with latitude. If the Earth were of uniform composition, such as granite, there would be simple, east-west, climatic zones resulting from variation in the amount of solar radiation that reaches different latitudes. At the continental level differential heating between land and ocean gives rise to distinctive continental climates with wider ranges of temperatures, lower humidity, and more variable precipitation than marine climates. The other primary energy source is the heat generated within the earth itself. It drives mantle convection and produces plate tectonics, causing mountain building. Mountainous areas are associated with the margins of the crustal plates, and the great elevation results from the upwarping of

the crust along the plate boundaries and the upwelling of magma that forms volcanic peaks and massive lava flows. The resulting mountains on the continents modify the climatic pattern that would otherwise develop on a flat continent. They are cooler and moister than surrounding lowlands and unbroken ranges of mountains are effective barriers to the passage of moisture. Mountains themselves have a typical sequence of elevation belts, with different ecosystems at different levels. These will differ according to the climate zone in which the mountains are embedded (see 5, above). Within the same macroclimate broad-scale landforms, other than high mountains, break up the east-west climatic patterns that would occur otherwise and provide a basis for further differentiation of ecosystems. At the local level topography causes variation in the amount of solar radiation received and in soil moisture regimes, both of which affect vegetation. The climate of the local area is perhaps best regarded as a topoclimatic variant of the particular macroclimate. The units derived from such an approach are termed “genetic” in that they are based on an understanding of how an ecosystem originated or evolved. As Rowe (1979) points out, the key to placing of map boundaries on ecological maps is understanding of genetic processes. We can only comprehend a landscape if we know how it originated or evolved. Knowing formative process is key in assessing possible impact that might be caused by land use and development.

16. *Criteria for setting ecoregion boundaries should be explicit in how regions are identified on the basis of comparable likenesses and differences.* Similar

ecoregions are found in similar latitudinal and continental locations (**Figure 4**). Therefore, the distribution of ecoregions is not haphazard; they occur in different parts of the world and can be explained in terms of the processes producing them. For instance, tropical/subtropical steppes are always located along the less arid margins of the tropical deserts on both north and south, and in places on the east as well; thus, the southwestern United States is similar to Argentina, central and southern Africa, and Australia. Because of this predictability, we can make assumptions about ecological features that can be transferred across similar ecoregions of the same continent or across analogous ecoregions on different continents. Some schemes of identifying ecosystems have been based on a gestalt approach to the recognition of homogeneous-appearing regions without considering the formative processes that differentiate them. Such methods identify each ecoregion as unique and unrelated to others. These are nothing more than "place name regions" such as the Great Plains of North America or the high altiplano of Bolivia or the Amazon rainforest, instead of being based on criteria that define what type of ecoregion each is. As a result analogous ecoregions in different continents or oceans may not be defined in the same way. Such inconsistency—defining ecoregions without specifying the factors upon which they were based—makes scrutinizing or confirming the regions difficult or impossible; and subsequently, results are difficult to communicate convincingly. We need a more explicit approach in which ecoregions are studied and classified on the basis of comparable likenesses and differences. Such explicit methods require us to consider the factors that underlie ecoregion differentiation.

Understanding the processes involved in ecoregion differentiation provides a basis for selecting significant criteria: those that are responsible for creating the range of ecoregion types found on the Earth.

17. *The limits of geographic ranges of species and races of plants and animals are not fully satisfactory criteria for determining the boundaries of ecoregions.* Sometimes the range limits for several species may coincide with an ecoregion boundary if that boundary follows some barrier that prevents range expansion, such as where plains meet mountains. Often, however, the range of a species does not stop abruptly at the border of an ecoregion, but continues for a distance into the adjacent ecoregion. The reason for this seems to be that some isolated areas of suitable habitat usually occur in the adjacent region. Furthermore, since at small map scales physiognomy (life form) is the best expression of ecological conditions (Küchler 1973, Gosz and Sharpe 1989), floristic and faunistic differences are best left to maps with other purposes. Because physiognomy is basic and applicable without exception anywhere on Earth, it has been selected to serve as the source for the criteria necessary to establish the basis for regional differences. These criteria permit a uniform approach throughout the world and put the various parts of the world on a comparable basis (see 16, above)

18. *Ecoregions should have greater ecological relevance than large physiographic land units*. The larger units are based on structural geology, although certain landform attributes, notably relief and degree of dissection, are also used

(Fenneman 1914). As stated earlier, climate plays a major role in ecosystem differentiation. Latitudinal position has a greater effect on the controlling climate than does geologically based physiography. As a result, many times the boundaries of such physiographic units cut across energy zones and their associated ecosystems. For example, the northern Great Plains in Canada will have a considerably different climate than the southern Great Plains in Texas. Therefore, the magnitude of the influences that physiography/substrate have on ecosystems also varies with latitude. Physiography appears to modify the climate within a latitudinal zone and therefore has a secondary effect on ecosystem differentiation (Swanson and others 1988).

19. *Ecoregion boundaries should have greater ecological relevance than watersheds (or basins or hydrologic units)*. Watersheds are based solely on which direction the water flows. Large areas of the globe have no clearly defined networks, and rivers often run through many areas of diverse topography that include many types of ecosystems (Omernik and Bailey 1997). The Platte River watershed in Colorado, for example, begins in the humid, high basins of the Rocky Mountains and flows through the rugged Front Range and into the semi-arid Great Plains. Depending on the ecoregion their watersheds are within, streams flowing into the Platte have very different thermal characteristics, gradients, aeration, and resultant biota. Ecoregions, therefore, can be very useful in management of watersheds by identifying areas within a watershed with similar aquatic ecosystems.

20. *The boundaries of ecoregions emerge from the study of spatial coincidences, patterning, and relationships, of climate, vegetation, soil, and landform.* This is preferred to the superimposing of thematic maps by automated geographic information systems that create complications because unit boundaries rarely conform to one another (Fosberg and others 1961, Bailey 1988b). This is also quite different from the numerical taxonomic method that uses cluster analysis of grid units to provide the map units. Furthermore, the boundaries cannot be derived mathematically from one or more data sets (cf., Host and others 1996) without understanding ecosystem pattern and process (see 14, above). Often, the best use of mathematical methods is after the fact, validating and refining land units when they have been mapped out by the application of ecological theory and good sense (Rowe and Sheard 1981). For example, I used discriminant analysis (Bailey 1984), a technique for analyzing *a priori* grouped data, to test whether two ecoregions in the conterminous United States were different on the basis of hydrologic productivity. The ecosystem regions tested in this study exhibited a high degree of ability to circumscribe a population of hydrologic stations with similar hydrologic productivity. A few stations were misclassified and may indicate where the boundaries, in terms of hydrologic productivity, may need some adjustment. Used in this way, quantitative methods can corroborate synthesis rendered by conceptual modeling and human integration of various information sources.

Limitations

As with the mapping of most natural phenomena, the division of the land surface into ecological regions, or zones, has limitations. First, strong internal variations (related to elevation, geology, and groundwater) may occur within zones; and boundaries between zones may be very irregular and much modified by human interference. Second, the boundaries of zones are slowly but continuously changing because of long-term alterations in the climate. [For a discussion of the effect of climate change on boundaries, see the series of papers in Holland and others (1991), as well as the article by Emanuel and others (1985).] Third, the zonal vegetation used to delineate the zones is based only on the undisturbed plant cover that is either known to exist or assumed to be able to grow should human intervention in the ecosystem cease.

The following principles apply to scarcely a quarter of our globe—the part that is high-and-dry terrestrial. The boundaries of terrestrial ecoregions are determined to a considerable extent by climatic factors. The same factors apply in differentiating the oceans into ecological regions (Bailey 1998a; Hayden and others 1984). Climate controls ocean hydrology, and thus marine ecosystem distribution. Understanding continental systems requires a grasp of the enormous influence that ocean systems exert on terrestrial climatic patterns, and thus the characteristics and distribution of continental ecoregions (Bailey 1998a). For example, there is more precipitation over the margins of continents bathed by warm water. The fact that we have warm-water currents along the East Coast of the United States explains why the mid-latitude deserts of the Southwest do not extend completely across North America. Therefore, I agree with Ray (1987) that any system of ecosystem regionalization that is solely terrestrial cannot be seriously entertained.

Application

These 20 principles perform as more than just written descriptors of ecoregion boundaries. They also serve as hinge points for interpreting data required to define ecoregions and their boundaries, plus they serve as test points for analyzing specific sites in field situations. Determining a landscape area’s legitimacy as an ecoregion depends not on satisfying some portion of these principles but in satisfying all of them.

Acknowledgements

I appreciate the helpful criticism of Stan Rowe, Dave Cleland, and Kevin Cook.

Literature Cited

Albert, D.A. 1995. *Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin*. Gen. Tech. Rep. NC-178. USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN. 250 pp.

Allen, T.F.H. and T.W. Hoekstra. 1992. *Toward a Unified Ecology*. Columbia University Press, New York. 384 pp.

Bailey, R.G. 1976. Map: *Ecoregions of the United States*. USDA Forest Service, Intermountain Region, Ogden, UT. Scale 1:7,500,000.

Bailey, R.G. 1983. Delineation of ecosystem regions. *Environmental Management* 7: 365-373.

Bailey, R.G. 1984. Testing an ecosystem regionalization. *Journal of Environmental Management* 19: 239-248.

Bailey, R.G. 1985. The factor of scale in ecosystem mapping. *Environmental Management* 9: 271-276.

Bailey, R.G. 1988a. *Ecogeographic Analysis: A Guide to the Ecological Division of Land for Resource Management*. Misc. Pub. 1465. USDA Forest Service, Washington, DC. 16 pp.

Bailey, R.G. 1988b. Problems with using overlay mapping for planning and their implications for geographic information systems. *Environmental Management* 12: 11-17.

Bailey, R.G. 1989. Ecoregions of the Continents—Scale 1:30,000,000 [map of land-masses of the world, published as a] supplement in *Environmental Conservation* 16 (4), 1989, and accompanying Explanatory Supplement to Ecoregions of the Continents (ibid. p 307-309).

Bailey, R.G. 1995. *Description of the Ecoregions of the United States*. 2nd ed. rev. and expanded (1st ed. 1980). Misc. Pub. No. 1391 (rev.). USDA Forest Service, Washington, DC. 108 pp., with separate map at 1:7,500,000.

Bailey, R.G. 1996. *Ecosystem Geography*. Springer-Verlag, New York. 216 pp., with separate maps of the oceans and continents at 1:80,000,000.

Bailey, R.G. 1998a. *Ecoregions: The Ecosystem Geography of the Oceans and Continents*. Springer-Verlag, New York. 186 pp., with separate maps of the oceans and continents at 1:80,000,000.

Bailey, R.G. 1998b. *Ecoregions Map of North America: Explanatory Note*. Misc. Pub. 1548. USDA Forest Service, Washington, DC. 10 pp., with separate map at

1:15,000,000, in cooperation with The Nature Conservancy and the U.S. Geological Survey.

Bailey, R.G. 2002. *Ecoregion-Based Design for Sustainability*. Springer-Verlag, New York. 240 pp.

Bailey, R.G. and H.C. Hogg. 1986. A world ecoregions map for resource reporting. *Environmental Conservation* 13: 195-202.

Borchert, J.F. 1950. The climate of the central North American grassland. *Annals Association of American Geographers*. 40: 1-39.

Box, E.O. 1981. *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography*. Dr. W. Junk Publishers, The Hague. 258 pp.

Burger, D. 1976. The concept of ecosystem region in forest site classification. In: *Proceedings, International Union of Forest Research Organizations (IUFRO)*. XVI World Congress, Division I: 20 June-2 July 1976; Oslo, Norway. IUFRO, Oslo, Norway: 213-218.

Cleland, D.T., P.E. Avers, W.H. McNab, M.E. Jensen, R.G. Bailey, T. King, and W.E. Russell. 1997. National Hierarchical Framework of Ecological Units. In: M.S. Boyce and A. Haney (eds.), *Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources*. Yale University Press, New Haven, CT. p. 181-200.

Clements, F. and V.E. Shelford. 1939. *Bioecology*. John Wiley & Sons, New York. 425 pp.

Commission for Environmental Cooperation. 1997. *Ecological regions of North America: Toward a common perspective*. Commission for Environmental Cooperation, Montreal, Quebec. 71 pp.

Crowley, J. 1967. Biogeography [in Canada]. *Canadian Geographer* 11: 312-326.

Damman, A.W.H. 1979. The role of vegetation analysis in land classification. *Forestry Chronicle* 55: 175-182.

Dice, L.R. 1943. *The Biotic Provinces of North America*. University of Michigan Press, Ann Arbor. 78 pp. with separate map at 1 inch equal 500 miles.

Ecoregions Working Group. 1989. *Ecoclimatic regions of Canada, first approximation*. Ecological Land Classification Series No. 23. Environment Canada, Ottawa. 119 pp., with separate map at 1:7,500,000.

Elder, J. 1994. The big picture: Sierra Club Critical Ecoregions Program. *Sierra* Mar./April: 52-57.

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

FAO 2001. Chapter 47, Global mapping. In: *Global Forest Resources Assessment 2000*. FAO Forestry Paper 140, Food and Agriculture Organization of the United Nations, Rome. p. 321-331.

Fenneman, N.M. 1914. Physiographic boundaries within the United States. *Annals Association of American Geographers* 4: 84-134.

Fosberg, F.R., B.J. Garnier, and A.W. Küchler. 1961. Delimitation of the humid tropics. *Geographical Review* 51: 333-347, with separate map at 1:60,000,000.

Foster, C.H.W. 2002. Reviving environmental regionalism. *Land Lines* 14(4): 7-19.

Gallant, A.L., E.F. Binnian, J.M. Omernik, and M.B. Shasby. 1995. *Ecoregions of Alaska*. U.S. Geological Survey Professional Paper 1567. U.S. Geological Survey, Washington, DC. 73 pp., with separate map at 1:5,000,000.

Gosz, J.R. and P.J.H. Sharpe. 1989. Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. *Landscape Ecology* 3: 229-243.

Hare, F.K. 1950. Climate and zonal divisions of the boreal forest formation in eastern Canada. *Geographical Review* 40: 615-635.

Hayden, B.P, G.C. Ray, and R. Dolan. 1984. Classification of coastal and marine environments. *Environmental Conservation*. 11: 199-207.

Hills, G.A. 1960. Comparison of forest ecosystems (vegetation and soil) in different climatic zones. *Silva Fennica* 105: 33-39.

Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science*. 105: 367-368.

Holland, M.M., P.G. Risser, and R.J. Naiman (eds.) 1991. *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments*. Routledge, Chapman & Hall, New York. 142 pp.

Host, G.E., P.L. Polzer, D.J. Mladenoff, M.A. White, and T.R. Crow. 1996. A quantitative approach to developing regional ecosystem classifications. *Ecological Applications* 6: 608-618.

Hudson, J.C. and E.B. Espenshade. 2000. *Goode's World Atlas*, 20th ed. Rand McNally, Chicago. 371 pp.

Hustich, I. 1953. The boreal limits of conifers. *Arctic* 6: 149-162.

Isachenko, A.G. 1973. *Principles of landscape science and physical-geographical regionalization* (trans. from Russian by R.J Zatorski, edited by J.S. Massey). Melbourne University Press, Carlton, Victoria, Australia. 311 pp.

James, P.E. 1959. *A Geography of Man*. 2d ed. Ginn, Boston. 656 pp.

Klijn, M. and H.A. Udo de Haes. 1994. A hierarchical approach to ecosystems and its implications for ecological land classification. *Landscape Ecology* 9:89-104.

Köppen, W. 1931. *Grundriss der Klimakunde.* Walter de Gruyter, Berlin. 388 pp.

Kruckeberg, A.R. 2002. *Geology and Plant Life: The Effects of Landforms and Rock Types on Plants*. University of Washington Press, Seattle. 362 pp.

Küchler, A.W. 1970. Potential Natural Vegetation. In: *National Atlas of the United States*. U.S. Geological Survey, Washington, DC. Scale 1:7,500,000.

Küchler, A.W. 1973. Problems in classifying and mapping vegetation for ecological regionalization. *Ecology* 54: 512-523.

Loucks, O. 1962. A forest classification for the Maritime Provinces. In: *Proceedings of the Nova Scotian Institute of Science.* Vol. 25, Part 2, 1962: 85-167, with separate map at 1 inch equals 19 miles.

McMahon, G., S.M. Gregonis, S.W. Waltman, J.M. Omernik, T.D. Thorson, J.A. Freeouf, A.H. Rorick, and J.E. Keys. 2001. Developing a spatial framework of common ecological regions for the conterminous United States. *Environmental Management* 28: 293-316.

Merriam, C.H. 1898. *Life Zones and Crop Zones of the United States*. Bulletin Division Biological Survey 10. U.S. Department of Agriculture, Washington, DC. p. 1-79.

Nature Conservancy, The. 1997. *Designing a Geography of Hope: Guidelines for Ecoregion-based Conservation in The Nature Conservancy*. The Nature Conservancy, Arlington, VA. Variable pagination.

Nielson, R.P. 1987. Biotic regionalization and climatic controls in western North America. *Vegetatio* 70: 135-147.

Nigh, T.A. and W.A. Schroeder 2002. *Atlas of Missouri Ecoregions*. Missouri Department of Conservation, Jefferson City, MO. 212 pp.

Nowacki, G., P. Spencer, M. Fleming, T. Brock, and T. Jorgenson. 2002. *Unified Ecoregions of Alaska: 2001*. Open File Report 02-297. U.S. Geological Survey, Washington, DC.

Olsen, D.M. and E. Dinerstein. 1998. The Global 2000: A representative approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology* 12: 502-515.

Omernik, J.M. 1987. Map supplement: Ecoregions of the conterminous United States. *Annals Association of American Geographers* 77: 118-125. Scale 1:7,500,000.

Omernik, J.M. and R.G. Bailey. 1997. Distinguishing between watersheds and ecoregions. *Journal American Water Resources Association* 33: 1-15.

Ray, G.C. 1987. Towards a world ecoregions map? *Environmental Conservation* 14: 80.

Rowe, J.S. 1979. Revised working paper on methodology/philosophy of ecological land classification in Canada. In: C.D.A. Rubec (ed.), *Applications of Ecological (Biophysical) Land Classification in Canada*. Ecological Land Classification Series No. 7. Environment Canada, Ottawa. p. 23-30.

Rowe, J.S. and J.W. Sheard. 1981. Ecological land classification: a survey approach. *Environmental Management*. 5: 451-464.

Schlutz, J. 1995. *The Ecozones of the World: the Ecological Divisions of the Geosphere* (trans. from German by I. and D. Jordan). Springer-Verlag, Berlin. 449 pp.

Schmidt, R.H. 1979. A climatic delineation of the 'real' Chihuahuan Desert region. *Journal of Arid Environments* 2: 243-250.

Swanson, F.J., T.K. Kratz, N. Caine, and R.G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *Bioscience* 38: 92-98.

Tansley, A.G. 1935. The use and misuse of vegetation terms and concepts. *Ecology*. 16: 284-307.

Thayer, R.L. 2003. *LifePlace: Bioregional Thought and Practice*. University of California Press, Berkeley, CA. 300 pp.

Trewartha, G.T. 1968. *An Introduction to Climate*. 4th ed. McGraw-Hill, New York. 408 pp.

Troll, C. 1966. Seasonal climates of the earth. The seasonal course of natural phenomena in the different climatic zones of the earth. In: E. Rodenwaldt and H.J. Jusatz (eds.), *World Maps of Climatology*, 3rd ed. Springer-Verlag, Berlin: 19-28, with separate map at 1:45,000,000 by C. Troll and K.H. Paffen.

Udvardy, M.D.F. 1975. *A Classification of the Biogeographical Provinces of the World*. Occasional Paper No. 18. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland. 48 pp.

Van Newkirk, A. 1975. Bioregions: towards bioregional strategy for human cultures. *Environmental Conservation* 2: 108.

Walter, H. 1985. *Vegetation of the Earth and Ecological Systems of the Geo-biosphere*. 3rd revised and enlarged ed. [trans. from German by Owen Muise]. Springer-Verlag, Berlin. 318 pp.

Walter, H. and E. Box. 1976. Global classification of natural terrestrial ecosystems. *Vegetatio* 32: 75-81.

Weaver, J.E. and F.E. Clements. 1938. *Plant Ecology*. 2nd edn. McGraw-Hill, New York. 601 pp.

Wright, R.G., M.P. Murray, and T. Merrill. 1998. Ecoregions as a level of ecological analysis. *Biological Conservation* 86: 207-213.

Table 1. Regional climates[a] and ecoregion equivalents

Köppen group and types	Ecoregion equivalents
A **Tropical and humid climates**	**Humid tropical domain** (400)
Tropical wet (Ar)	Rainforest division (420)
Tropical wet-dry (Aw)	Savanna division (410)
B **Dry climates**	**Dry domain** (300)
Tropical/subtropical semi-arid (BSh)	Tropical/subtropical steppe division (310)
Tropical/subtropical arid (BWh)	Tropical/subtropical desert division (320)
Temperate semi-arid (BSk)	Temperate steppe division (330)
Temperate arid (BWk)	Temperate desert division (340)
C **Subtropical climates**	**Humid temperate domain** (200)
Subtropical dry summer (Cs)	Mediterranean division (260)
Humid subtropical (Cf)	Subtropical division (230) Prairie division (250)[b]
D **Temperate climates**	
Temperate oceanic (Do)	Marine division (240)
Temperate continental, warm summer (Dca)	Hot continental division (220) Prairie division (250)[b]
Temperate continental, cool summer (Dcb)	Warm continental division (210) Prairie division (250)[b]
E **Boreal climates**	**Polar domain** (100)
Subarctic (E)	Subarctic division (130)

F **Polar climates**

Tundra (Ft)	Tundra division (120)
Ice Cap (Fi)	Icecap division (110)

Definitions and Boundaries of the Köppen-Trewartha System

Ar	All months above 18^{o}C and no dry season.
Aw	Same as Ar, but with 2 months dry[c] in winter.
BSh	Potential evaporation exceeds precipitation, and all months above 0^{o}C.
BWh	One-half the precipitation of BSh, and all months above 0^{o}C.
BSk	Same as BSh, but with at least 1 month below 0^{o}C.
BWk	Same as BWh, but with at least 1 month below 0^{o}C.
Cs	8 months 10^{o}C, coldest month below 18^{o}C, and summer dry.
Cf	Same as Cs, but no dry season.
Do	4 to 7 months above 10^{o}C, coldest month above 0^{o}C.
Dca	4 to 7 months above 10^{o}C, coldest month below 0^{o}C, and warmest month above 22^{o}C.
Dcb	Same as Dca, but warmest month below 22^{o}C.
E	Up to 3 months above 10^{o}C.
Ft	All months below 10^{o}C.
Fi	All months below 0^{o}C.

A/C boundary = Equatorial limits of frost; in marine locations, the isotherm of 18^{o}C for coolest month.
C/D boundary = 8 months 10^{o}C.
D/E boundary = 4 months 10^{o}C.
E/F boundary = 10^{o}C for warmest month.
B/A, B/C, B/D, B/E boundary = Potential evaporation equals precipitation. Boundary,
$R = \frac{1}{2}T - \frac{1}{4} PW$
Where R = rainfall, in.
T = temperature, ^{o}F
PW = % annual rainfall in winter half year
Desert/steppe boundary is
$R = \frac{1}{2} T - 1/4PW/2$
or half the amount of the steppe/humid boundary

[a] Based on the Köppen system of classification (1931), as modified by G.T. Trewartha

(1968).

[b] Köppen did not recognize the Prairie as a distinct climatic type. The ecoregion classification system represents it at the arid sides of the Cf, Dca, and Dcb types, following Borchert (1950).

[C] A dry month is defined as the month in which the total precipitation expressed in millimeters is equal to or less than twice the mean temperature in degrees Celsius.

Table 2. Change of preferred positions of three-tree species[a] on the normal moisture regime, but with three different topoclimates for the seven most easterly site regions of Ontario, Canada[b]

		Topoclimate	
Site region	Hotter	Normal	Colder
1	P		
2	P		P
3	P		p
4	A	P	P
5	A		A P
6	C		A P
7			C A

---

[a] P = *Picea glauca* (white spruce); A = *Acer saccharum* (sugar maple); C = *Carya ovata* (shagbark hickory)

[b] From Burger (1976)

Figure captions

Figure 1. The mosaic of prairie and oak forest in the so-called “Prairie Peninsula” (black), as mapped by Küchler (1970).

Figure 2. Map of the saltbush-greasewood vegetation type, which occurs primarily on halomorphic soils, scattered over arid and semi-arid regions of the western United States. Adapted from Küchler (1970).

Figure 3. Ecoregional boundary dividing forested mountain ranges and intermontane valleys, with sagebrush steppe, from low-lying plains, with sagebrush steppe, along the Snake River, Idaho. Potential natural vegetation from Küchler (1970); ecoregional boundary from Bailey (1995).

Figure 4. Generalized global pattern of tropical/subtropical steppes (black), as mapped by Bailey (1989).

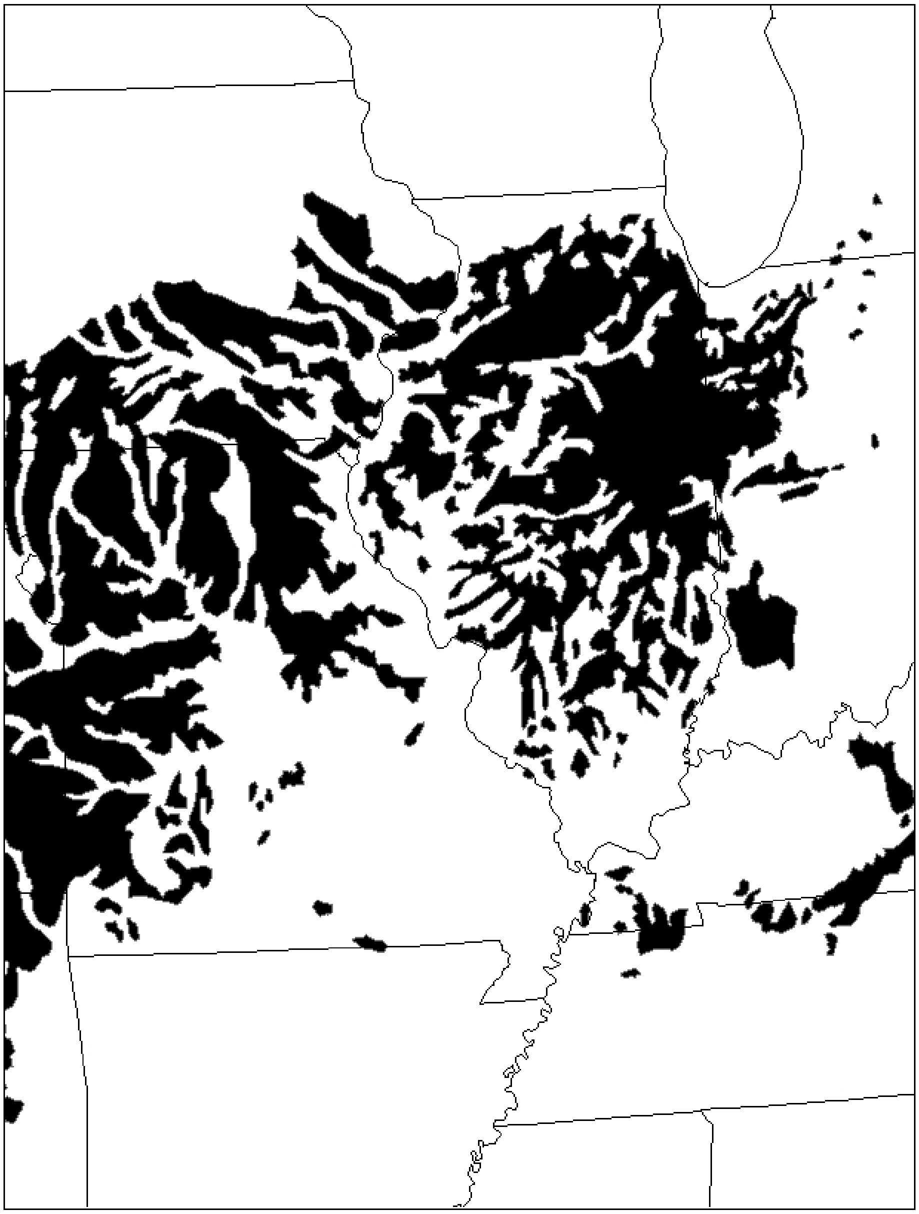

Figure 1

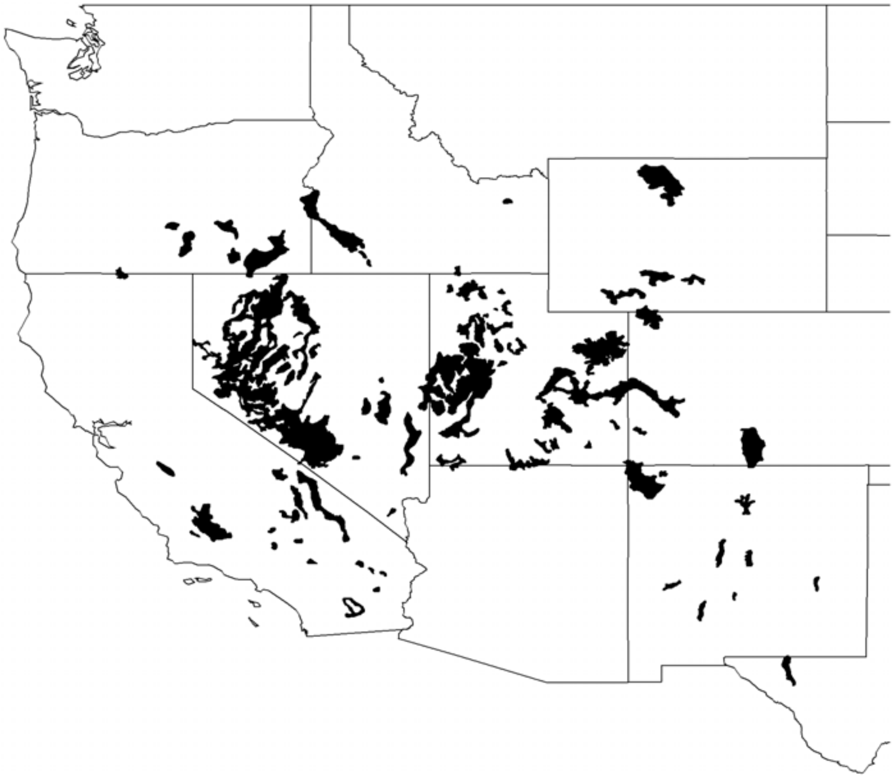

Figure 2

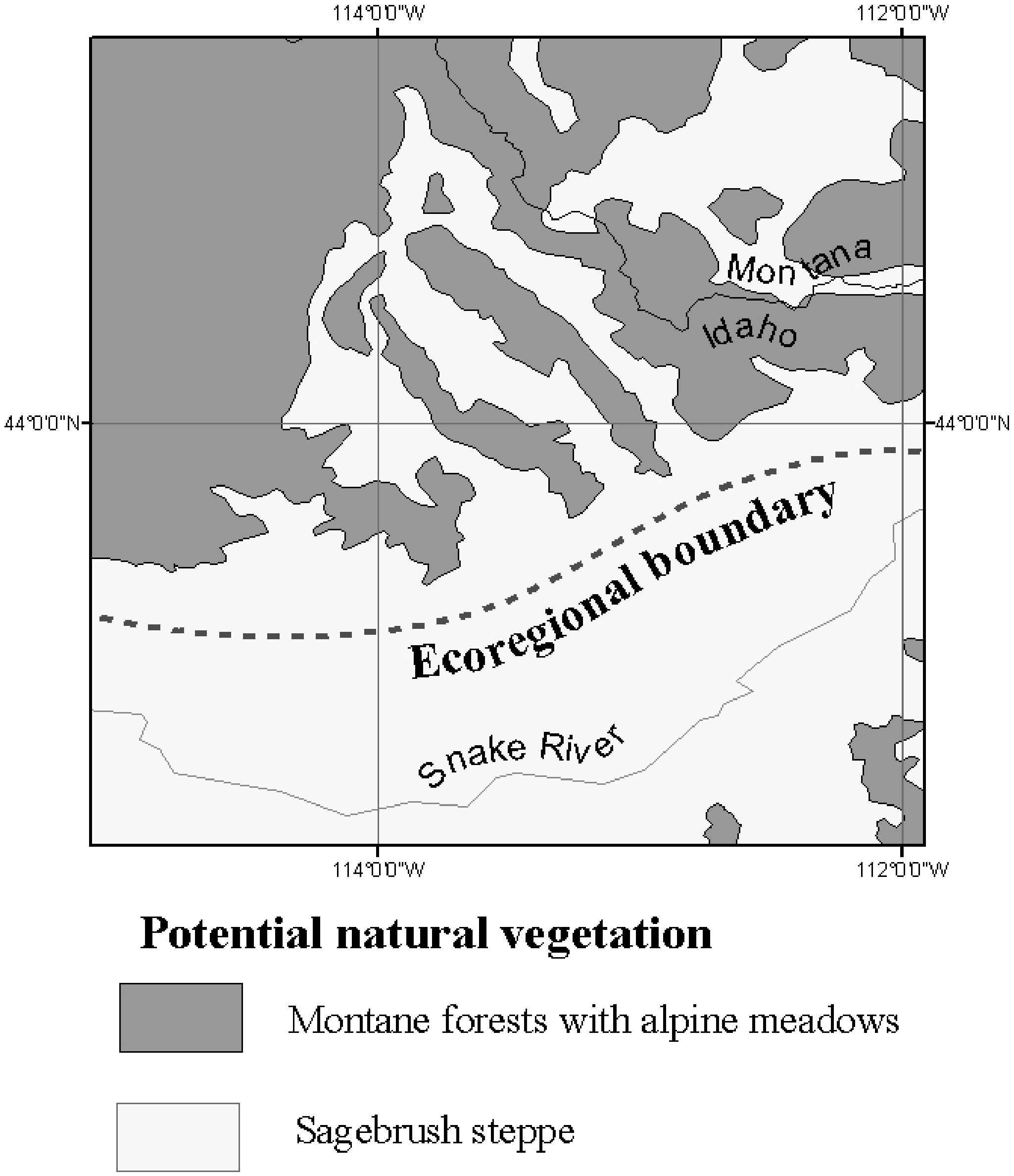
114°0'0"W
112°0'0"W
44°0'0"N
44°0'0"N
Montana
Idaho
Ecoregional boundary
Snake River
114°0'0"W
112°0'0"W
Potential natural vegetation
Montane forests with alpine meadows
Sagebrush steppe

Figure 3

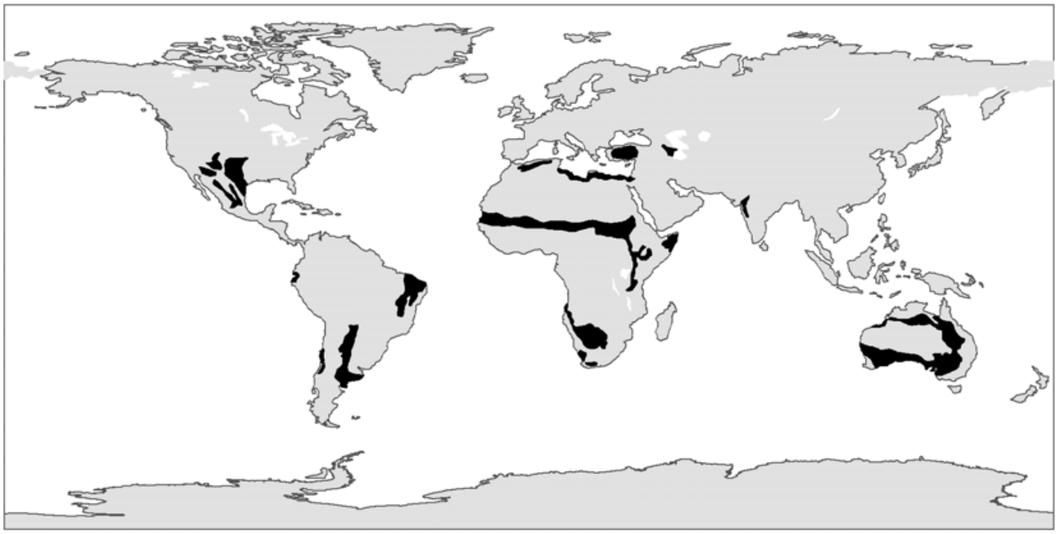

Figure 4