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The Holdridge life zones of the conterminous United States in relation to ecosystem mapping

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Abstract

Aim Our main goals were to develop a map of the life zones for the conterminous United States, based on the Holdridge Life Zone system, as a tool for ecosystem mapping, and to compare the map of Holdridge life zones with other global vegetation classification and mapping efforts.

Location The area of interest is the forty-eight contiguous states of the United States.

Methods We wrote a PERL program for determining life zones from climatic data and linked it to the image processing workbench (IPW). The inputs were annual precipitation (Pann), biotemperature (T_{bio}), sea-level biotemperature (T_0bio), and the frost line. The spatial resolution chosen for this study (2.5 arc-minute for classification, 4-km for mapping) was driven by the availability of current state-of-the-art, accurate and reliable precipitation data. We used the Precipitation-elevation Regressions on Independent Slopes Model, or PRISM, output for the contiguous United States downloaded from the Internet. The accepted standard data for air temperature surfaces were obtained from the Vegetation/Ecosystem Modelling and Analysis Project (VEMAP). This data set along with station data obtained from the National Climatic Data Center for the US, were used to develop all temperature surfaces at the same resolution as the Pann.

Results The US contains thirty-eight life zones (34% of the world's life zones and 85% of the temperate ones) including one boreal, twelve cool temperate, twenty warm temperate, four subtropical, and one tropical. Seventy-four percent of the US falls in the 'basal belt', 18% is montane, 8% is subalpine, 1% is alpine, and $<0.1\%$ is nival. The US ranges from superarid to superhumid, and the humid province is the largest (45% of the US). The most extensive life zone is the warm temperate moist forest, which covers 23% of the country. We compared the Holdridge life zone map with output from the BIOME model, Bailey's ecoregions, Küchler potential vegetation, and land cover, all aggregated to four cover classes. Despite differences in the goals and methods for all these classification systems, there was a very good to excellent agreement among them for forests but poor for grasslands, shrublands, and nonvegetated lands.

Main conclusions We consider the life zone approach to have many strengths for ecosystem mapping because it is based on climatic driving factors of ecosystem processes and recognizes ecophysiological responses of plants; it is hierarchical and allows for the use of other mapping criteria at the association and successional levels of analysis; it can be expanded or contracted without losing functional continuity among levels of ecological complexity; it is a relatively simple system based on few empirical data; and it uses objective mapping criteria.

Keywords

Ecosystem management, frost line, Holdridge, life zones, United States, vegetation mapping

INTRODUCTION

A fundamental first step in designing ecosystem management is the delineation and classification of ecologically homogeneous units. To identify the basic attributes of the system being managed it is possible that such attributes could be derived from existing maps or classification schemes. This is a difficult task at any level of biological (organisms to associations) or ecological complexity (life zones to latitudinal belts), or at any spatial scale from a small watershed to the entire United States. Past efforts to classify and map ecosystems of the United States include vegetation maps based on ecological studies, such as those for the eastern region by Braun (1950), maps of biomes based on bio-geographical criteria by J. Aldrich of the U.S. Fish and Wildlife Service (Smith, 1974; pp. 536–537), maps of potential vegetation based on local knowledge and temperature criteria (e.g. Küchler, 1964) and maps of 'life zones' based on temperature criteria such as Merriam's (1898) life and crop zone map. For early comparisons of these approaches see Odum (1945) and Daniel *et al*. (1979).

Bailey has undertaken the most comprehensive effort to classify and map ecosystems of the United States. He devised a hierarchical classification of ecosystems using the methods of geographers (Bailey, 1980, 1983, 1984, 1985, 1987, 1988, 1989, 1995, 1996). This particular approach has been adopted by many U.S. Government agencies (Bailey, 1988, , 1995; McNab & Avers, 1994) and will receive particular attention in this article. Another similar effort is that of Omernik (1995) who mapped the ecological areas and ecological regions of the United States.

The availability of computerized techniques for handling large, spatially referenced data bases (e.g. geographical information systems [GIS]), has increased greatly our power to predict and map patterns of potential natural vegetation. For example, the BIOME model (Prentice *et al*., 1992) predicts potential vegetation based on variables such as mean coldest-month temperature, growing season temperature, a drought index incorporating seasonality of precipitation, and available water capacity of the soil. With a combination of satellite imagery and computer analysis techniques, it is now possible to map actual vegetation for most parts of the world as has been done for US forests (Powell *et al*., 1993) and land cover (Loveland *et al*., 1991).

Each of these efforts has strengths and weaknesses, and they are all used for some aspect of ecosystem management (cf. Daniel *et al*., 1979). For example, the satellite images of land cover are excellent for assessing ecosystems at particular moments in time, but they require continuous updating because land cover and uses change constantly. Satellite images are also useful for validating land-cover and land-use models and for monitoring purposes. Traditional vegetation mapping, which focused on mature or climax vegetation (Whittaker, 1956) and maps of potential vegetation (Küchler, 1964) are useful for comparing actual vegetation with potential or mature vegetation and for assessing magnitudes of change as a result of disturbances. However, the process of constructing these types of maps often involves circular reasoning. In the absence of comprehensive climatic information, vegetation is used *de facto* as a surrogate of climate. However, climate in turn is a driver of climax vegetation (Odum, 1945; Daubenmire, 1956; Whittaker, 1956). This problem also permeates many of the bio-geographical approaches to ecosystem mapping (Bailey, 1996).

Another problem is that many traditional vegetation classification systems are not sufficiently objective so that different people do not always produce the same classification designation for a particular geographical space. Part of the problem is that many of these classification systems are not driven by empirical data and consider the natural driving forces upon ecosystems only weakly. Moreover, these classification systems require users to have experience with the applicability and quality of the data base, and then fail to provide explicit rules for deciding how to use information to classify ecosystems (Bailey & Hogg, 1983). The result is that two people using the same information can produce different ecosystem classification maps. The maps themselves have gone through rapid evolution (Bailey, 1976, 1989, 1996; Bailey & Cushwa, 1981; Bailey *et al*., 1994).

The Holdridge system for classifying world life zones or plant formations (from now on Holdridge Life Zone System; Holdridge, 1967) overcomes many of the aforementioned weaknesses of available ecosystem classification systems and can be a useful tool for identifying ecological units (life zones). The Holdridge Life Zone System is simple and objective requiring at the minimum only data on mean annual precipitation, mean annual biotemperature (T_{bio}), and elevation. We have three objectives in this paper: (1) to define the qualities of an ecosystem classification system for mapping in relation to ecosystem management and show how the Holdridge Life Zone System fulfills most of these requirements; (2) to develop and describe a life zone map for the conterminous United States; and (3) to compare the map of Holdridge life zones with other classification and mapping efforts such as those for ecoregions, global biome models (BIOME), potential vegetation, and land cover.

QUALITIES OF AN ECOSYSTEM CLASSIFICATION SYSTEM

Managing ecosystems involves managing the structure and function of ecological units *sensu* Tansley (1935) and Evans (1956). The complexity implied in this task can be made more effective if the units of management are as ecologically homogeneous as possible. This in turn depends on the effectiveness of the classification system. Classification systems that result in ecologically homogeneous units should be more effective than those that result in ecologically heterogeneous units because management treatments tend to be uniform and the response of a homogeneous system is more likely to be uniform than that of a heterogeneous system. The classification system must be the following.

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Based on geo-referenced quantitative data. The more empirically driven the system is, the less subjective it will be and the more potential it has for improvement as more and better quality data become available.

As objective as possible. It is impossible for an ecosystem classification system to be completely objective because we lack complete knowledge about the geographical distribution of variables used for classifying ecological units. Subjectivity will be reduced by the degree to which a classification system is empirically driven and by stating classification rules and assumptions explicitly.

Reflect as closely as possible the forces driving ecosystems. Ecosystems are basic units of ecology with arbitrary physical boundaries (Evans, 1956). Ecosystem function is driven primarily by climatic factors, followed by edaphic, geomorphic, and biotic factors. Therefore, ecosystem classification systems that reflect the driving forces of ecosystems closely are more likely to define the functional units of ecology than those that attempt to define particular states or uses of ecosystems (i.e. forest or land-use types), or particular ecosystem size classes (i.e., 10^5 km^2 ecoregions).

Hierarchical. Ecosystem function is hierarchical and includes chemical, biological, ecological, and extraterrestrial hierarchies of complexity. An ecosystem classification system has to be hierarchical and contain units of classification that can be aggregated or subdivided as seamlessly as possible so that by changing the level of complexity few discontinuities in the functioning and structuring of the system are introduced. Arbitrary hierarchies based on rules of size or area, i.e. powers of 10, contain too much ecological heterogeneity and no matter how convenient size hierarchies might be, their use introduces discontinuities and reduce the effectiveness of ecosystem management. A manager may treat an ecosystem type as if it was a homogeneous unit when in fact it may be heterogeneous. The occurrence of homogeneous units of ecological function is size-independent and can be one, or one thousand square kilometers in area. In fact, Whittaker (1953) stated (p. 56): 'Areal extent is irrelevant to achievement of the climax steady state, however; and there is no lower limit on the area of a climax type.'

Convenient for expanding or contracting complexity scales. Because ecosystem management takes place at many scales of ecological complexity, an ecosystem classification scheme should be flexible and capable of expanding or contracting to greater or lesser scales of complexity. This is achieved by aggregating or segregating its classification units while maintaining continuity with the functioning of the resulting ecosystems.

Useful for anticipating global climate change. The environment in which natural resources managers now operate requires sensitivity to global climate change. To satisfy this requirement the system has to be based on measures of climate so that a reliable base condition can be established. Then change can be evaluated relative to that base condition. Changes cannot be detected or established objectively if ecosystem states are compared to a subjective or continuously shifting initial condition.

Applicable to all the world. Because there are no boundaries to the function of ecosystems in the biosphere, an ecosystem classification system has to be applicable to the whole world. This means that it has to account for changes in ecosystem functioning across latitudinal belts.

Demonstrably valid. An ecosystem classification system should be validated with independent ecological data.

Conform to principles of climatic classification and vegetation function. Climate is a major driver of vegetation distribution and ecosystem functioning (Schimper, 1903). An ecosystem classification system must be based on climatic factors, including climatic extremes and seasonality. An example is the treatment of frost, which is critical for delimiting tropical and subtropical ecosystems and determining the distribution and richness of species (Schimper, 1903; Holdridge, 1967). The treatment of montane areas also requires special attention as they are climatically heterogeneous (Daubenmire, 1952, 1956) and contain complex environmental gradients (Brown & Curties, 1952; Hayward, 1952; Oosting & Reed, 1952; Whittaker, 1956, 1960).

Accepts new data as a means to sharpen the analysis. Ecosystem science is a rapidly evolving field which requires that ecosystem classification systems be open for improvement. Ideally, a map designation should change only as new empirical data become available.

THE HOLDRIDGE LIFE ZONE SYSTEM

The main advantage of the Holdridge Life Zone System (Fig. 1) is that it is empirically and objectively based. Life zones are the main ecological unit of classification and they define conditions for ecosystem functioning. Life zones are delimited by biotemperature, precipitation, potential evapotranspiration ratio, and elevation (see methods for definitions and explanations). Any person using the system and having access to the same data will classify a life zone the same way. There is little room for subjectivity. The life zone system is hierarchical in that life zones can be subdivided into *associations* according to site conditions including more detailed climatic data, atmospheric conditions, edaphic conditions, topography, and aspect (Holdridge, 1967). Associations can be subdivided further into successional stages that reflect land use, management, or disturbance history. Life zones can be aggregated into larger humidity provinces, or belts of altitude and/or latitude. The latitudinal belts reflect the utility of the system for global scale ecosystem classification, while the altitudinal belts show it application to the complex montane conditions.

The Holdridge Life Zone System contains ecological and ecophysiological constraints. For example, Holdridge reasoned

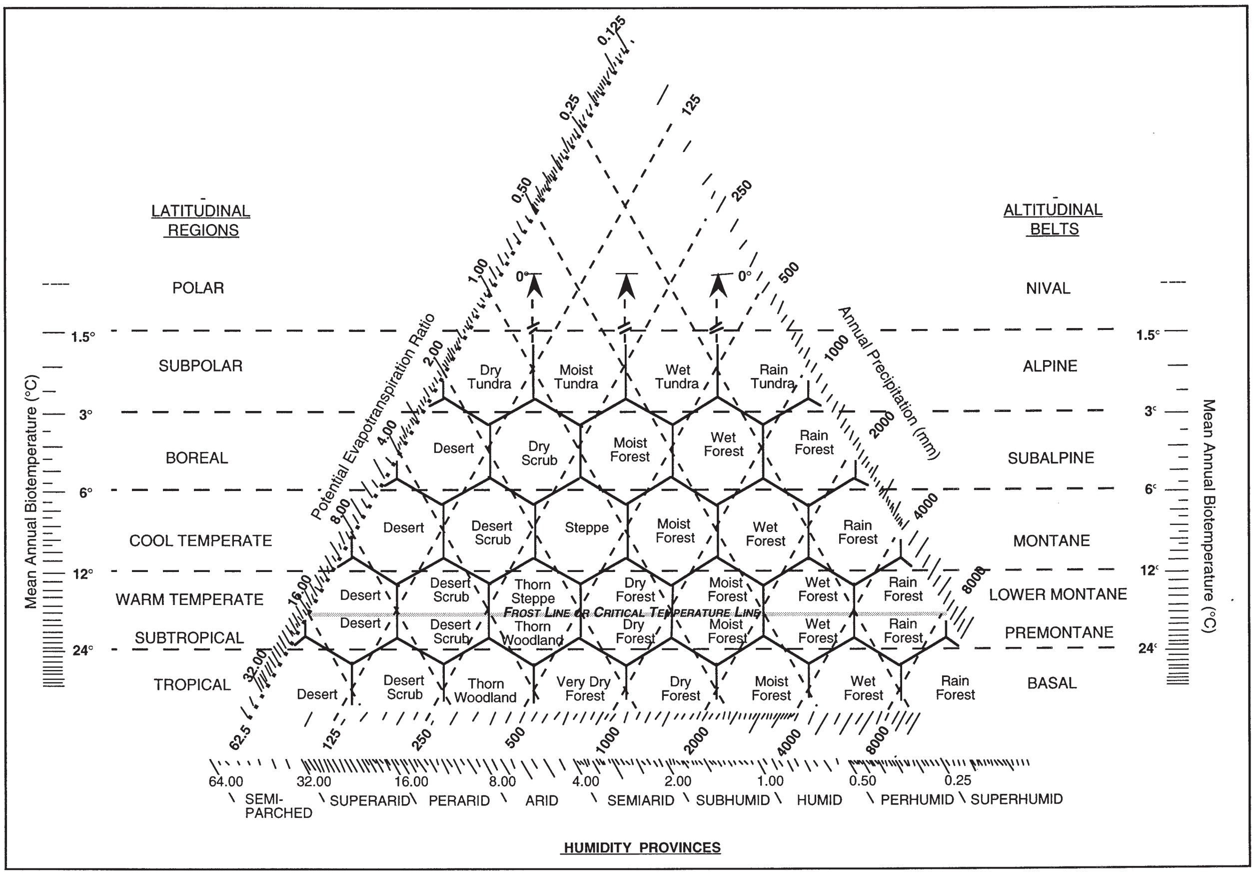

Figure 1 The life zone chart of Holdridge (1967). Consult text for further explanation.

that net primary productivity ceases at temperatures below 0 °C and above 30 °C. The ratio of potential evapotranspiration to precipitation reflects water availability for ecological functions. The relationship between climatic parameters and life zone delineation are logarithmic in recognition of limiting factor kinetics (Holdridge, 1967).

The Holdridge Life Zone System has been used to map the life zones of some 20 countries, including parts of the United States (Sawyer, 1963; Sawyer & Lindsey, 1964; Brown & Lugo, 1980). A life zone map of the world has also been produced and used to estimate the effects of global climate change on the distribution of life zones (Emanuel *et al.*, 1985); however, the resolution of the map was coarse, altitudinal belts were not considered, and attention to frost or limiting temperature line was poor.

The Holdridge Life Zone System has been criticized for three reasons: (1) it is viewed as a system for classifying only tropical ecosystems (2) life zone names do not always coincide with observed vegetation, i.e. grasslands appear in areas classified as forests, and (3) it does not consider the seasonality of climatic parameters. The first criticism is not valid as evidenced by the mapping of the world life zones for application to global climate change issues (Emanuel *et al.*, 1985; Solomon & Shugart, 1993); the early work of Sawyer (1963), and Sawyer & Lindsey (1964) in the United States; and the work we report here.

With regards to the second criticism, L.R. Holdridge addressed this in a letter to A.A. Lindsey as follows:

'The life zone system does not or should not pretend to delineate homogeneous communities or associations of vegetation. The life zone is a climatic division defined by biotemperature, precipitation, potential evapotranspiration, and elevation in a logarithmic system which makes all life zones equivalent in significance. Within each life zone there may be several vegetation associations dependent on soils, lesser climatic variables and the presence or absence of open water. The one climatic association of each life zone wherein none of the secondary variations are significant, corresponds to a zonal soil and zonal climate. This, of course, may or may not be present in an area where the life zone is present, but since the physiognomy of the climatic association most clearly typifies the life zone it has been utilized on the chart as a name for the life zone.'

In other words, the Holdridge life zone map depicts the climatic conditions for ecosystem function and not the state of the land at a particular time. The name of the life zone is not intended to mean that a particular vegetation is to be found in a particular location. For example, the llanos of Venezuela are classified as tropical dry forest, but a considerable fraction of the vegetation is tropical savanna due to edaphic conditions (Ewel & Madriz, 1968). Thus, while the climate could support forest growing on a zonal soil, the local conditions modify the response of vegetation into savanna. These situations are resolved at the association, rather than the life zone, level of the hierarchy.

The third criticism of the Holdridge Life Zone System is correct as climatic seasonality is not considered when identifying life zones at the first level of the hierarchy. This problem becomes critical when comparing two regions with similar average annual precipitation and biotemperature but where one of them has a strong seasonality of rainfall or where one has a wet winter and dry summer (e.g. in the western USA). This situation would have to be resolved at the level of the association when other climatic variables are assessed.

The designation of Holdridge life zones automatically includes consideration of their water balance and thus, the inputs of rainfall and outputs of runoff and evapotranspiration are incorporated into the classification. Wetlands, including mangroves, respond to life zone conditions (Lugo & Cintrón, 1975; Weaver, 1987; Lugo *et al*., 1995). However, to assess the effect of life zones in aquatic ecosystems fully, one has to consider the relative influence of the different life zones within the watershed boundaries of the aquatic system.

The Holdridge Life Zone System has been used for numerous ecosystem management applications or to organize data, including: evaluation of the effects of potential global climate change on vegetation distribution (Emanuel *et al*., 1985; Solomon & Shugart, 1993), carbon storage in tropical forests (Brown & Lugo, 1982), analysis of global soil carbon and nitrogen content (Post *et al*., 1982, , 1985), land use and management (Tosi, 1980), evaluation of human population distributions (Tosi & Voertman, 1964), and other issues such as predicting land productivity (Tosi, 1980) or evaluating ecosystem complexity and species richness (Lugo & Brown, 1991).

Life zone maps for the eastern and central United States have been developed (Sawyer, 1963; Sawyer & Lindsey, 1964) but they were based on a limited amount of information, particularly climatic data for locations at high elevations. In Sawyer's early work, he found eleven life zones within four latitudinal regions (cool temperate, warm temperate, subtropical, and tropical) in the eastern and central United States. A particular problem with this early effort was the omission of life zones at high elevations due to a lack of data. Sawyer & Lindsey (1964) observed that scale difficulties prevented them from showing life zones that covered small areas at higher elevations. Today, with larger and more extensive data bases, GIS technology, and fast computers, it is possible to make maps with greater accuracy and precision so that life zones with limited geographical extension can be identified. Technological development is another argument in favour of classifying ecosystems based on geo-referenced data because it allows managers to be more precise in their assessments.

METHODS

Climate data

Precipitation

The spatial resolution chosen for this study (2.5 arc-minute for classification, 4-km for mapping) was driven by the availability of accurate, reliable, documented, and archived precipitation data. The current state-of-the-art in spatially distributed precipitation modelling is provided by the Precipitation-elevation Regressions on Independent Slopes Model or PRISM (Daly *et al*., 1994). The latest version of PRISM output for the contiguous United States was downloaded from the Internet (ftp://fsl.orst.edu/pub/daly/prism/). This data set contains monthly long-term average (1961–90) precipitation totals at a 2.5 arc-minute grid resolution. The data set also provides the Digital Elevation Model (DEM) which was used to interpolate the precipitation data within the PRISM model.

Temperature

Air temperature surfaces were obtained from the Vegetation/Ecosystem Modelling and Analysis Project (VEMAP) (ftp://ftp.ucar.edu:/cgd/vemap/). This accepted-standard data set provides monthly long-term average minimum and maximum air temperature surfaces for the contiguous United States at a 30-arc-minute (approximately 50 km) grid resolution, derived from measurements at 4613 meteorological stations (Kittel *et al*., 1995). These temperature surfaces were enhanced to a finer grid resolution by distributing the 30-arc-minute temperature data over the topography of the 2.5-arc-minute DEM from the PRISM data set. Using the Neutral Stability Algorithm, a method of spatial interpolation that explicitly accounts for the relation between elevation and temperature (Dodson & Marks, 1997), the centroids of the 30-arc-minute temperature grid cells were interpolated to the resolution of the PRISM DEM, resulting in a set of air temperature surfaces which are compatible with the PRISM precipitation data (i.e. which correspond to the same 2.5 arc-minute DEM). Monthly mean air temperature surfaces were obtained by averaging the minimum and maximum surfaces for each month.

Frost line

The presence of frost defines the boundary between the warm temperate and subtropical life zones in the Holdridge classification. A frost line (delineation of frost-free and frost-prone zones) was developed for the contiguous United States from long-term daily measurements of minimum air temperature. Daily meteorological station data were obtained from the National Climatic Data Center (ftp://ftp.ncdc.noaa.gov/pub/data/fsod/) where the data are maintained, documented, and archived. Stations that did not have at least 20 full years of daily minimum temperature data during the period 1960–95 were excluded, leaving 394 stations that were distributed reasonably evenly across the United States. The average number of frost days per year was computed for each station location:

$$\mathrm{Fmean} = \frac{\mathrm{sum(Fdays)}}{\mathrm{Nyears}} \tag{1}$$

where Fmean is the mean number of frost days per year, Fdays is the number of days where Tmin was less than 0.0 C, and Nyears is the length of the climate record in years. The 394 point measurements of Fmean were interpolated to a 4-km grid by inverse-squared-distance (using eight nearest neighbours, no maximum distance). A more elaborate elevation-sensitive interpolation was not used here because (1) the sparseness of the stations do not warrant it and (2) the boundary between warm temperate and subtropical regions in the USA is restricted to the lower elevations. The no-frost zone was then defined as the set of grid cells where Fmean is less than 0.5, i.e. cells which averaged less than one frost day per year (for at least 20 years in the period 1960–95). The 4-km frost line grid was projected to a 2.5-minute latitude/longitude grid for compatibility with the temperature and precipitation surfaces.

We followed this procedure without exception for our map. We are generally confident that that this procedure projected the frost line well, except for areas in south Florida where we know from experience that frost events with considerable ecological effects occur (Olmsted *et al.*, 1993). With improved temperature data it will be possible to better define the frost line and thus adjust the location of subtropical and tropical life zones in south Florida.

Biotemperature

Biotemperature (T_{bio}) was computed from the monthly mean temperature surfaces (Holdridge, 1967) as follows:

$$T_{bio} = \frac{\text{sum(Tavg[i] if } 0 < \text{Tavg[i]} < 30\text{; else 0)}}{12 \ \{i = 1 \ldots 12\}} \quad (2)$$

where i indexes the months January through December and Tavg(i) is the mean temperature (°C) of a grid cell for a given month. Sea-level biotemperature was computed by applying a lapse rate of –6.0 °C/km (as used by Holdridge, 1967) to the mean temperatures and then using equation 2. Grid cell elevations were defined by the PRISM DEM.

A set of biotemperatures was also computed from daily temperature measurements to evaluate the robustness of computing T_{bio} from monthly, rather than daily, data; and also to validate the 2.5-minute temperature surfaces. Daily Tmax measurements were obtained from the corresponding Tmin stations used in estimating the frost line. The number of stations which satisfy the 20-year constraint for both Tmin and Tmax was 241. For each station, biotemperature (T_{bio}) was computed from daily minimum and maximum temperature (Holdridge, 1967) as follows:

$$T_{bio} = \text{sum}\{[(\text{Tmin[i] if} > 0\text{, else 0}) + (\text{Tmax[i] if} < 30\text{, else 30})]/2\}/N \ \{i = 1 \ldots N\} \quad (3)$$

where i indexes each day in the climate record (minimum 20 years), Tmin[i] and Tmax [i] are the observed minimum and maximum temperatures (°C) on day i, and N is the total number of days in the climate record. The relationship between the 241 T_{bio} from daily station data and from the monthly surface data is skewed slightly from the 1:1 line (Fig. 2). For T_{bio} below about 15 °C, the monthly T_{bio} begins to show a bias toward colder temperatures. We checked the elevations of the measurement stations and their corresponding DEM grid cells and verified that this bias was due not simply to differing elevation values. The mean elevation difference was 10.8 m (standard deviation of 62 m) and the mean absolute difference was 19.6 m (root mean square error of 62.6).

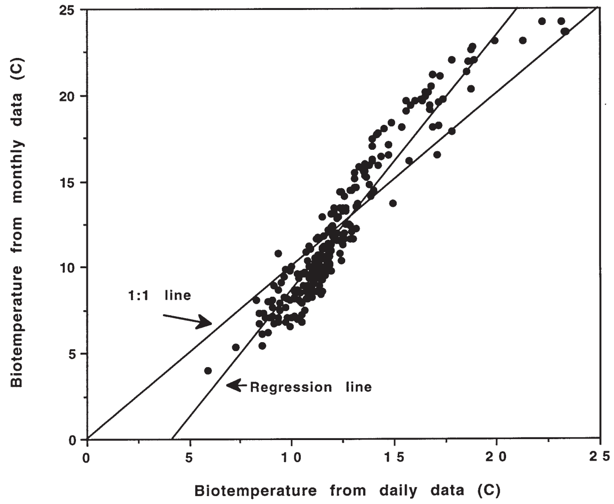

Figure 2 Relation between mean annual biotemperature (T_{bio}) based on daily station data and that based on monthly surface data ($n = 241$, $r^2 = 0.96$; see text for further details).

Life zone classification

We wrote a program for determining life zone designations in PERL programming language, and linked it to the image processing workbench (IPW) (Frew, 1990; Longley *et al.*, 1992). The inputs are biotemperature (T_{bio}), sea-level biotemperature (T_0bio), frost line, and annual precipitation (Pann). The classification algorithm involved locating an input cell in ‘Holdridge hexagon space’ (Fig. 1), which is a 2-d lattice of hexagons bounded by logarithmic axes of biotemperature, annual precipitation, and potential evapotranspiration ratio (PETR). The PETR was derived as (T_{bio} * 58.93)/Pann (Holdridge, 1967). The life zone type (e.g. moist forest, steppe, desert) for each map pixel was determined by the hexagon centroid which is closest to the input cell. The latitudinal region (polar, subpolar, boreal, cool temperate, warm temperate, subtropical, tropical) was determined by the sea-level biotemperature and, if applicable, by the presence of frost. The altitudinal belt (nival, alpine, subalpine, montane, lower montane, premontane) was determined by the actual biotemperature (as opposed to sea-level temperature). In the Holdridge System, biotemperatures for the basal altitudinal and latitudinal belts have correspondence along a logarithmic progression from 1.5° (nival and polar) to 24° (basal and tropical). Thus, if the actual and the sea-level T_{bio} corresponded to the same latitudinal region, then the altitude belt was null, i.e. the basal belt.

We applied a ‘fuzzy’ classification rule to the derivation of latitudinal region to avoid the situation where a very small

Table 1 Biotemperature (T_{bio}) thresholds for latitudinal regions. See text for the meaning of terms.

Latitudinal regions	Original	Fuzzy
Subpolar	1.5	1.68
Boreal	3.0	3.36
Cool temperate	6.0	6.72
Warm temperate/Subtropical	12.0	13.44
Tropical	24.0	26.89

change in sea-level T_{bio} changes the overall life zone classification. For example, a site with Pann = 500 mm, T_{bio} = 5.95 °C, and T_0bio = 6.05 °C would be classified, under the traditional method, as 'cool temperate subalpine moist forest', although the difference between actual and sea-level T_{bio} was caused by an elevation of only 17 m (using the –6 °C/km lapse rate). Under our fuzzy rule, the sea-level T_{bio} is not permitted to change the life zone unless it extends far enough into the next latitudinal region to be significant. 'Significant' threshold values were defined as the T_{bio} value of the lower-most hexagon vertex of each row of hexagons in Holdridge space (Table 1). Thus, under the fuzzy rule, the example site would be classified as 'boreal moist forest'.

RESULTS

The United States has thirty-eight life zones (Fig. 3) or 34% of the world's total (Lugo & Brown, 1991). These life zones span five latitudinal belts from tropical to boreal (Fig. 4a) and five altitudinal belts from lowland to nival (Fig. 4b), and range from desert to rain forest in terms of moisture extremes (Table 2, Fig. 4c). The United States has representatives of 85% of the temperate life zones of the world (Table 2). Among the latitudinal belts, the most extensive is warm temperate which covers 64% of the country, followed by the cool temperate (35%; Table 2). The lowlands comprise 72% of the territory and include nineteen life zones. There are six montane life zones which comprise 18% of the territory while eight subalpine life zones comprise 9% of the territory (Table 2).

The life zone with the largest area is the warm temperate moist forest which covers 1.78 Mkm^2 or 23% of the area of the United States (Fig. 3). The life zone with the smallest areal coverage is the warm temperate alpine moist tundra, covering only 32 km^2. Several areas are fairly homogeneous from a climatic point of view: south-eastern United States with seven life zones, north-eastern United States with four life zones, and the central United States with three life zones. The western United States is extremely heterogeneous with thirty-six life zones or 95% of all the life zones in the country.

Tropical and subtropical life zones occur only in the southern tip of Florida and in the south-west coast of California (Fig. 4a) where tree species such as mangroves and other tropical hardwoods grow. While we have mapped south Florida according to the data base we used (methods), we recognize that part of these life zones should be considered warm temperate. The single boreal life zone occurs in the Cascade Mountains of northern Washington.

DISCUSSION

We examined four other types of ecosystem classification systems and maps to verify and evaluate the Holdridge map. These other classification systems included: the Loveland *et al.* (1991) land-cover map based on AVHRR (Advanced Very High Resolution Radiometer) satellite images, Baileys ecoregions map, BIOME model output (Prentice *et al.*, 1992), and Küchlers (1964) potential vegetation map. Although all these maps attempt to classify the land in some way, they do so from different perspectives, thus one would not expect perfect agreements among them. For example, Bailey's map classifies large scale ecological units much like the life zone map does, BIOME's map shows model output of potential vegetation based on similar climatic variables as the life zone system, Loveland *et al.* s map shows present land cover/land use, and Küchler's map shows potential vegetation.

All maps were aggregated to four categories to allow for a common base of comparison (forest, crop land, grassland, and shrubland; Fig. 5) and the Kappa-statistic (Monserud & Leemans, 1992) was computed for all classes overall as well as for individual classes (Table 3). There was fair to good agreement overall among the maps, except with Loveland *et al.*'s. It is not surprising that Loveland *et al.*'s map had the poorest agreement among all because it shows present day land cover/land use which was not the goal of any of the other classification systems. The map that most closely agreed with the life zone map was BIOME (Kappa = 0.47), once again not too surprising because they are both based on similar climatic variables. When the four maps were compared with the life zone map within the four land cover classes (Table 3), they displayed very good to excellent agreement for forests, and very poor to poor agreement for grasslands, shrublands and nonvegetated land. Again the Holdridge life zone map and the BIOME map were similar to each other despite the simplicity of the Holdridge system compared to the highly complex model that generates BIOME, and the relatively coarse scale resolution of the BIOME output (0.5° × 0.5°).

The generally low overall agreement among these maps should not be used as arguments for selecting one map over another; the low agreement underscores the danger of using maps for applications they are not designed for. The Holdridge life zone map depicts the conditions that regulate ecosystem function and not the actual vegetation type or state of the land at a particular time. Actual vegetation is mapped in the Holdridge Life Zone system at the levels of plant association and successional status. The AVHRR land-cover map depicts the use of the land as it was at the time the satellite imagery was acquired. Bailey's map is derived from Küchler's and thus they are similar to each other, but Bailey's ecoregions aggregate large areas and miss the subtleties of most natural land cover.

Compared with Bailey's ecoregions, the Holdridge life zone map provides more resolution as it shows smaller ecological units that are lumped in the Bailey system due to the size-limit rules (Fig. 6). The depiction of latitudinal belts is also dramatically different as the Bailey system shows a large fraction of the United States classified as subtropical while the life zone map does not. This is because the life zone system uses a strict definition of subtropical (the critical temperature

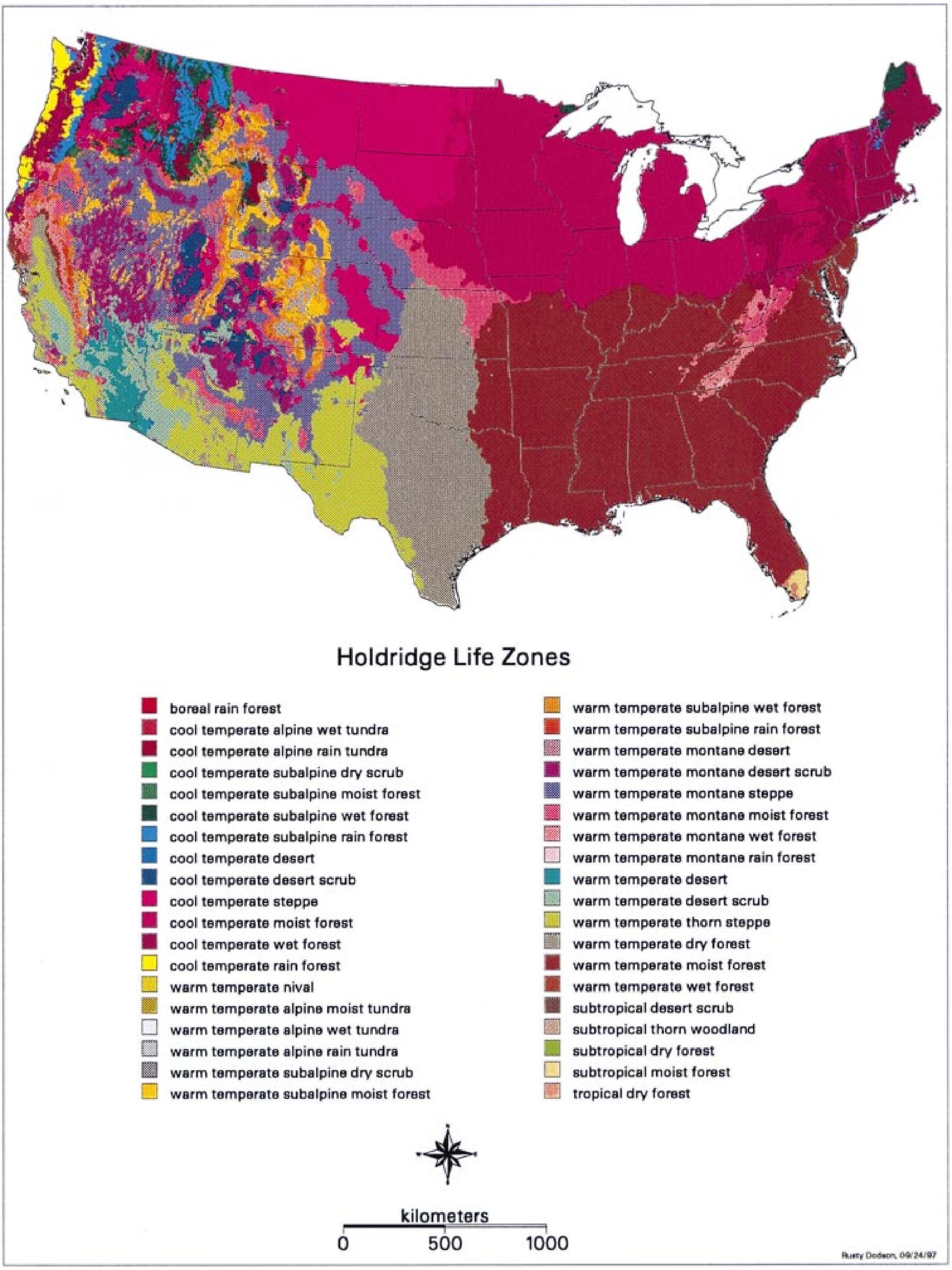

Figure 3 Life zone map for the United States based on enhanced VEMAP climate data; 2.5 arc-minute resolution or approximately 4 km × 4 km resolution.

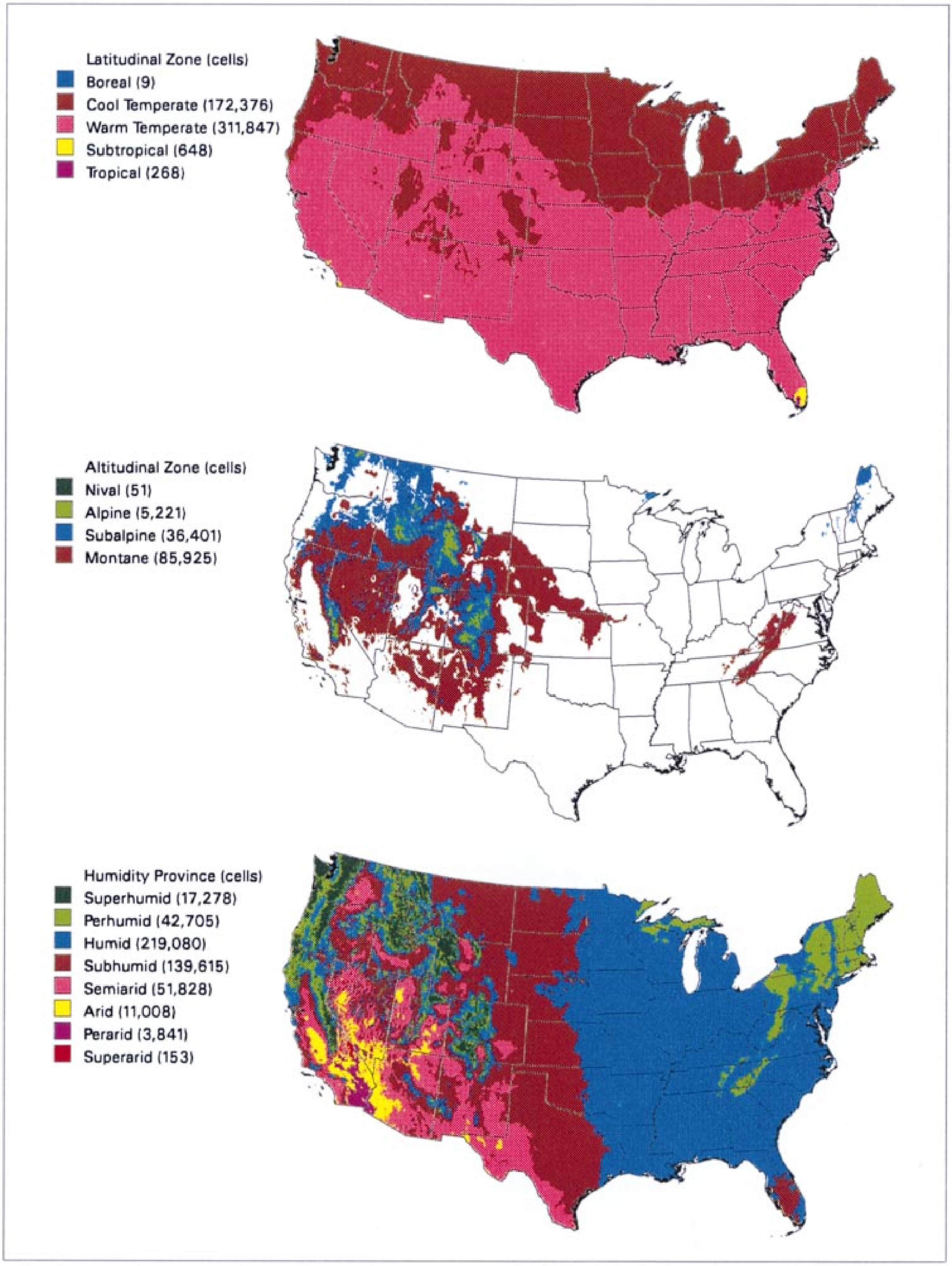

Figure 4 Life zones of the United States aggregated by (a) latitudinal zones (b) altitudinal zones (white is the basal zone), and (c) humidity provinces.

Table 2 Percentage distribution of life zones in the United States. The total area covered by the ife zones is 776.8 Mha.

Life zone grouping	Number of life zones	% of total area
Latitudinal		
Tropical	1	0.1
Subtropical	4	0.1
Warm temperate	20	64.3
Cool temperate	12	35.5
Boreal	1	< 0.1
Altitudinal		
Basal	18	73.7
Montane	6	17.7
Sub-alpine	8	7.5
Alpine	5	1.1
Nival	1	< 0.1
Humidity Provinces		
Superarid	1	< 0.1
Perarid	1	0.8
Arid	3	2.3
Semiarid	4	10.7
Sub humid	7	28.8
Humid	7	45.1
Per humid	8	8.8
Super humid	7	3.6
Total for USA	38	100

of frost line; Fig. 1) while the Bailey system does not. In fact, subtropical divisions appear as subsets of temperate domains in maps of the ecological subregions of the United States (McNab & Avers, 1994). Such mixing of latitudinal designations makes it very difficult to interpret latitudinal variation in the Bailey classification system, as one expects the latitudinal designations to be segregated in space as they do naturally, and not to appear as subsets of one another. The Bailey system also does not depict the large number of ecological units in western United States.

Ecosystems can be mapped in a variety of ways according to the purpose of the mapping. We argue that for the purposes of ecosystem management, ecosystems must be mapped from the point of view of the factors that regulate their structure and function because that is what management is trying to manipulate. Among other things, ecosystem managers strive to alter productivity, regeneration, material cycling, and stability of ecosystems (Lugo *et al.*, 1999). The ecosystem concept itself is based on function as defined by Evans (1956; p. 1127): '. . . an ecosystem involves the circulation, transformation, and accumulation of energy and matter through the medium of living things and their activities.' This is why the category 'ecosystem' cannot appear as an entity in a biological or ecological hierarchy. Ecosystems occur at all levels of complexity in the hierarchy. Therefore, it stands to reason that classifying ecosystems from a functional perspective will both facilitate and increase the effectiveness of ecosystem management because the units of management are more likely to be structurally and functionally homogeneous than they would when they are classified by other criteria. Classifying ecosystems by geographical area or size is particularly troubling because it forces rigid size rules on systems characterized by complex environmental gradients and diversity patterns that are unrelated to size (Whittaker, 1953).

Early ecologists strove to classify plant communities by criteria easily obtainable at that time such as vegetation physiognomy, taxonomic composition, geographical location, or generalized perceptions of climate and edaphic variability. Robert H. Whittaker (1953) formalized the notion of environmental gradients to explain the distribution of vegetation and pointed out that criteria based on geographical area (size), physiognomy, taxonomy, and other such indicators were unsatisfactory to explain function and at times resulted in circular reasoning. Whittaker (1970) published ordinations of ecosystems along gradients of mean annual temperature and precipitation but he did not attempt to place map boundaries for the vegetation types except for the particular locations that he studied (Whittaker, 1956, 1960). As a result of Whittaker's research, it is possible to differentiate between geographical space (place), the biota which temporarily occupies geographical space, and ecological gradient space (*sensu* Hall *et al.*, 1992) which drives biotic processes. The Holdridge Life Zone System formalizes the identification of ecological space, i.e. it identifies the climatic conditions that result in particular ecosystem functioning over particular geographical space.

Geography-based ecosystem mapping as described by Bailey (1996) and Omernik (1995) use climatic, land-form, vegetation, and soils information as well as hierarchical concepts to map ecosystems worldwide. But these efforts have limited value for assessing ecosystem functioning because they do not consistently address the driving factors of ecosystems and place too much significance on size or space-driven hierarchies (Bailey, 1985). Their focus is on mapping geographical space and the objects on that space at a particular time without sufficient consideration of the variation or gradients of climate over their spatial units. The result is that the Bailey and Omernik system of ecosystem classification mixes different kinds of ecosystems in the same management category.

In the Bailey mapping effort, the Köppen system, as modified by Threwartha, is used as the climatic input data. The reason Köppen is used is because it is the international standard system of classification for geographical purposes (Bailey, 1995, , 1996). However, this system of climate classification, while of great value for geographical purposes, is not necessarily adequate for representing the climatic diversity of the world. The Köppen system aggregates climate categories to such an extent that it oversimplifies the complexity of the world's climate, particularly in locations such as the western United States and throughout all the tropics and subtropics. For example, Bailey, based on Köppen, defines the rainforest division as located between the equator and 10N with an annual mean temperature close to 27°C. Hawaii is given as an example of this division, but Hawaii is at latitude 18°N and its average temperature for the coolest and warmest month is 21–24°C. As another example, the temperate region and tropical/subtropical dry regions are differentiated by winter temperatures. The tropical/subtropical climate is defined as that where temperatures in the coolest month are warmer than 0°C but colder than 18°C and has eight months or more warmer than 10°C. For the temperate

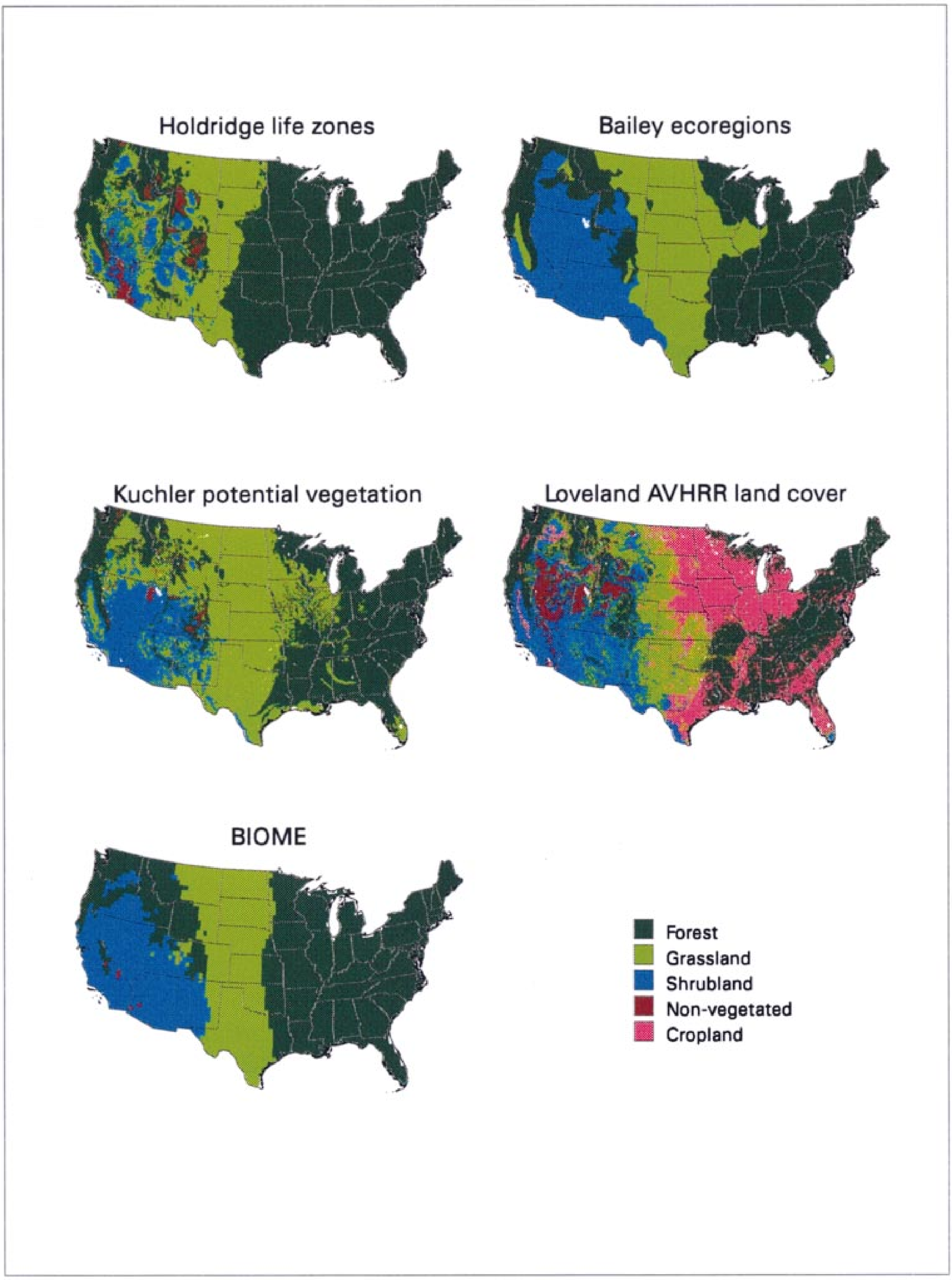

Figure 5 Maps of aggregated land cover classes of the United States according to Holdridge, Bailey, Küchler, Loveland AVHRR, and BIOME.

Table 3 Degree of agreement among the different classification maps and the Holdridge Life Zone map based on the Kappa-statistic (Monserud & Leemans, 1992)*.

a. Overall Kappa	Holdridge	Bailey	Kuchler	Loveland
Holdridge	1.0			
Bailey	0.39	1.0		
Kuchler	0.43	0.69	1.0	
Loveland	0.25	0.41	0.37	1.0
BIOME	0.47	0.71	0.60	0.37

b. Kappa by vegetation group	Holdridge			
	Forest	Grassland	Shrubland	Non-vegetated
Bailey	0.83	0.21	0.24	–
Kuchler	0.87	0.26	0.29	0.39
Loveland	0.87	0.41	0.16	0.07
BIOME	0.76	0.42	0.22	0.44

* Kappa statistic: 0.00–0.05 = no agreement; 0.05–0.20 = very poor; 0.20–0.40 = poor; 0.40–0.55 = fair; 0.55–0.70 = good; 0.70–0.85 = very good; 0.85–0.99 = excellent; 0.99–1.00 = perfect agreement

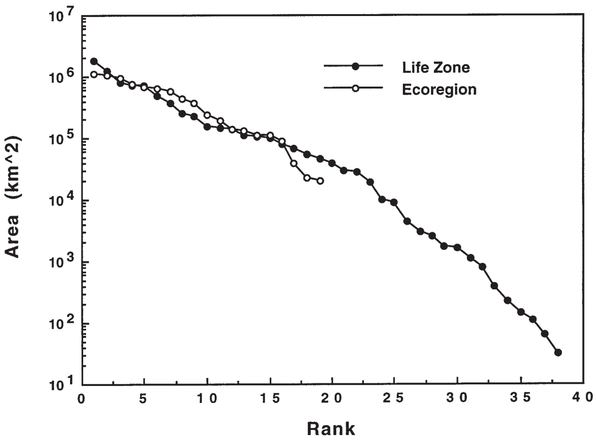

Figure 6 Rank order by area of the thirty-eight life zones of the United States and the ecological provinces of Bailey *et al.* (1994).

climate, on the other hand, the coldest month is cooler than 0°C and has 4–8 months warmer than 10°C. This definition of subtropical/temperate climates ignores the presence of regular frost which is the critical factor that delimits the distribution of tropical/subtropical species from temperate ones. The result is that Bailey's ecoregion maps show the United States as a country with a very high representation of tropical/subtropical regions, but without the biodiversity associated with these climates.

In presenting the life zones of the United States, we have shown how to take advantage of empirical data bases to define the life zone condition over a geographical space upon which ecosystems function. This removes subjectivity in mapping while at the same time defining the potential and limits for ecosystem functioning on that site. Size or area prejudgements are removed and the ecosystem manager can deal directly with the biota of interest. On this climatic foundation other modifying factors can be overlain as required of any hierarchical system of ecosystem classification and management.

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