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APPLYING BIOGEOGRAPHIC PRINCIPLES TO RESOURCE MANAGEMENT: A CASE STUDY EVALUATING HOLDRIDGE'S LIFE ZONE MODEL

James A. MacMahon* and Thomas F. Wieboldt1,2

ABSTRACT.—Conservation schemes require some portioning of the world into a discrete number of subunits which might benefit from similar management practices. The Holdridge Life Zone scheme, proposed for such purposes previously, is applied to Utah as an initial test of its usefulness. A hypothetical life zone map was developed entirely on the basis of weather station data and data derived from these values. This predictive map compared favorably to data on patterns of vegetation, mammal, reptile, and amphibian distribution in Utah.

Since the publication of MacArthur and Wilson's (1967) analytical approach to the biogeography of islands, several authors have attempted to apply island biogeography theory to the problem of optimum size and number of nature reserves.

Several aspects of theory have been invoked including species/island area relations (Diamond 1975, Sullivan and Shaffer 1975, Wilson and Willis 1975) and extinction rates (Terborgh 1974). Not all authors agree that this approach is correct or robust (Simberloff and Abele 1976). [See also rebuttals to Simberloff and Abele, e.g., Diamond (1976)]. Simultaneously the theories of island biogeography are being changed or restated in verifiable formats (Simberloff 1976).

Currently economics (Myers 1976) and even international cooperation (Franklin 1977) are being included as factors in nature reserve establishment. Despite all of the interest in the application of theory to practical problems there are few attempts to provide a reasonable plan to test the efficacy and appropriateness of the implied theory/practice merger.

Recently, without judging whether or not theory was adequate or correct, MacMahon (1977a) suggested a series of concrete steps one might opt to test the various hypotheses. It was hoped that this would be applicable on a world scale.

In summary the suggestion was to determine the most sensitive species to be preserved (i.e., rarest, largest, highest trophic level, most vagile, etc.). This species determines the minimum size of the reserve area. One might also, for a community, use the species area relationship (MacArthur and Wilson 1967). That relationship is

$$S = CA^z$$

where $S =$ number of species, $A =$ island area, $C =$ parameter characteristic of a particular taxon and archipelago and $z =$ power derived by assuming species abundances are distributed in a log normal manner (Preston 1962). The value of $C$ is a community coefficient and not known for most communities. One must also invoke consideration of extinction rates for determining the number of replicate areas necessary (Terborgh 1974).

MacMahon pointed out that if the total world variety of communities was reduced into some small grouping to determine functions like $C$ and determine whether or not there is similar value of $C$ for most ex-

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1Wieboldt reduced some data for this paper. He did not prepare the manuscript and should not be held accountable for the content.

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amples of communities within one of these groups, then the conservation process could proceed more rapidly and be applied more broadly.

The suggestion was made that a possible system of classification, often used but seldom tested, was that of Holdridge (1947, 1967). Holdridge's scheme uses mean annual biotemperature (the sum of mean monthly temperature above 0°C divided by 12), mean annual precipitation and potential evapotranspiration to place localities on a chart divided into hexagons representing vegetation types (Fig. 1). Corrections are made for altitudinal differences at similar latitudes (Holdridge 1967, Sawyer and Lindsey 1963, Tosi 1964) (Fig. 2).

The hexagonal areas are termed life zones. When a specific site is located on the Holdridge model, a trinomial designation corresponding to its latitudinal position, altitudinal belt, and humidity province is applied. If the station lies in the basal altitudinal belt, the latitudinal region alone is used with the humidity province. An example will illustrate this procedure. Logan, Utah, lies at an elevation of 4,790 ft (1460 m), has a mean annual biotemperature of 10.0°C and a mean total annual precipitation of 16.64 inches (423 mm). Using the standard lapse rate of 6°C per thousand meters, a mean annual sea level biotemperature of 18.76°C is calculated corresponding to the subtropical latitudinal region (Fig. 2). The actual biotemperature of 10.0°C corresponds to the montane altitudinal belt (Fig. 2). The lines for a 10.0°C biotemperature and 423 millimeters precipitation intersect within the steppe life zone (Fig. 1). The trinomial life zone designation of Logan, Utah, would be subtropical montane steppe.

The question is, do all communities of the world falling into a particular life zone, e.g., subtropical montane steppe, have similar values of C and can they be treated in the conservation sense in a similar way?

![Graphical model to assign life zone designations to localities based on three abiotic measurements (after Holdridge 1967).](image)

Fig. 1. Graphical model to assign life zone designations to localities based on three abiotic measurements (after Holdridge 1967).
Note that we are aware that the evolution of species, major taxa differences, and the specific species-species interactions in the various examples of particular life zones will all dictate detailed differences from place to place. Despite this, the question remains—is there a least common denominator of similarity such that not every community in the world will have to be studied before it can be conserved? If ecological laws really exist this least common denominator should be identifiable at some level of resolution, albeit generalized.

The first step in answering the specific question at hand is to ascertain whether or not the Holdridge model is applicable simultaneously to plants and animals (communities), outside of the tropics and in an area where sufficient climatic and distribution data are available.

Since the few tests of the Holdridge model by people outside the Holdridge group (see review Holdridge et al. 1971) suggest its plausibility for vegetation (Lindsey and Sawyer 1970, Sawyer and Lindsey 1963, 1971, Thompson 1966), tropical birds (Slud 1960, 1976), and tropical reptiles and amphibians (Heyer 1967), a more detailed faunal and vegetational test seems appropriate. We report here on an attempt to answer the question whether life zones predicted on Holdridge's model do coincide with the patterns of distribution of animals and plants in nature to a significant degree.

**Methods**

Data from 68 weather stations, selected from throughout Utah and having long climatic records (i.e., a minimum of 30 year averages of monthly temperatures and annual precipitation based on 1931-1960 records) were the main data base to generate the "theoretical life zones" of Utah. Re-
Records of longer duration are available for certain stations. In these cases averages based on the total years of record are used. Records of shorter duration are used wherever climatological data gaps occurred in critical geographic areas.

Fig. 3. Predicted potential life zone map of Utah. Assignment of localities to Holdridge life zones derived entirely from abiotic data based on United States Weather Bureau data corrected as described in the text.
Temperature and precipitation data provide only a rough approximation of the life zones because of topographic and physiognomic complexity. Maps of available heat, potential evapotranspiration, and normal annual precipitation from Jeppson et al. (1968) provided information to correct for these irregularities. Additionally, we had access to precipitation data from the United States Forest Service, Dixie National Forest, snow survey data from the Soil Conservation Service, and data reported in the literature (Price and Evans 1937). All of these data were used to derive estimates of values of the three factors necessary to define the hypothetical life zones of a particular locality.

The development of certain regression relationships (Figs. 9, 10) permitted us to take point data and derive yearly values and thus estimate life zone boundaries where few weather stations were available. This was particularly valuable because Utah weather stations are generally in the valleys. The station data or calculated points were plotted on a life zone chart (Fig. 1). Names were applied to life zones using the altitudinal and latitudinal corrections (Fig. 2). Life zone designations were then used to generate a theoretical life zone map (Fig. 3).

To determine whether or not the hypothetical life zones coincided with existing or potential life zones, several maps were generated or used.

The recent vegetation map of Cronquist et al. (1972), interpreted in light of Küchler's (1964) map, was used as the vegetation standard (Fig. 4). Additionally maps were prepared of conifer (Fig. 5) and some semiarid shrub (Fig. 6) distributions. Conifer distributions are taken from Little (1971). Shrub distributions are based on field data, unpublished dissertations, and analysis of herbarium specimens at Brigham Young University and Utah State University.

Maps of mammal biotic provinces (Fig. 7) were adapted from Durrant (1952), while a series of reptile and amphibian maps were drawn (Fig. 8) based on data in Stebbins (1966). These two groups of vertebrates were used because they represent taxa of relatively high habitat fidelity, relatively low vagility (compared to birds), and well-known distributions, and they represent a range of physiologies (e.g., ectotherms vs. endotherms).

**Results and Discussion**

The "hypothetical" life zone map derived entirely from estimates of abiotic factors according to the Holdridge (1967) scheme is presented in Fig. 3.

A comparison of Fig. 3 to the Utah vegetation map (Fig. 4) reveals interesting similarities and differences. The vegetation map is more detailed in the Great Basin desert (western one-half of the state) area and the Canyonlands floristic section (southeastern one-fourth) than the hypothetical map. In mountainous regions (Montane Zone, Fig. 4) the hypothetical map is more detailed. These differences are merely matters of scale in some cases and map basis in others. Much of the Great Basin desert mosaic is undoubtedly due to edaphic factors in the Cronquist et al. (1972) presentation. Since the vegetation map relies on species distributions, shadscale (Atriplex confertifolia) vs. sagebrush (Artemisia tridentata) communities are differentiated even though they may be in similar climate zones.

In the montane areas the Cronquist map, because of scale, recognizes one community while the hypothetical map includes topographically related climatic changes and predicts community differences. Similar reasoning explains the Canyonland area discrepancies between the two maps.

An integrated interpretation of the maps suggests a high degree of coincidence. The creosote bush vegetation zone clearly coincides with an isolated part of the Subtropical Lower Montane Desert Scrub. The Subtropical Montane Desert Scrub plus Subtropical Montane Steppe clearly coincides with the sagebrush plus shadscale vegetation
Fig. 4. Vegetation map of Utah redrawn from Cronquist et al. (1972) and modified slightly with reference to field notes and the map of Küchler (1964).
zones. The Canyonlands floristic section coincides well with large sections of the Subtropical Lower Montane Desert Scrub.

The Absolute Desert vegetation zone coincides with Subtropical Montane Desert.

Finally there is high overlap of the aggregated montane hypothetical life zones and the Montane vegetation zone.

Analysis of conifer distributions (Fig. 5), mainly montane forms, in conjunction with

Fig. 5. Distribution outlines of 10 conifers in Utah (adapted from Little 1971). Species include Abies concolor, A. lasiocarpa, Juniperus communis, J. scopulorum, Picea engelmannii, P. pungens, Pinus contorta, P. flexilis, P. ponderosa, Pseudotsuga menziesii.
the hypothetical map (Fig. 3) shows surprisingly close fits of species boundaries and hypothetical life zone boundaries. This fit is biologically more meaningful than the recognition of a single montane vegetation for the purpose of predicting management practices. It is well known that steep topographic gradients cause community bound-

Fig. 6. The distribution limits of 13, mainly semiarid woody plants with limits in southern Utah. Data derived from unpublished theses, dissertations, and analysis of herbarium specimens and field notes. Species include: Berberis fremontii, Encelia frutescens, Fraxinus anomala, Yucca angustissima, Yucca baccata, Lycium pallidum, L. torreyi, Coleogyne ramosissima, Quercus undulata, Dalea fremontii, D. lanata, D. polyadenia, and D. thompsonae.
aries to become discrete when they otherwise form continua (Beals 1969). The vegetation map is generalized beyond management usefulness in the area of mountains.

The non-Great Basin desert semiarid woody plants mapped (Fig. 6) approximate the distribution of the Subtropical Lower Montane Steppe plus Subtropical Lower Montane Desert Scrub hypothetical life zones. The Mojave desert section of Utah (extreme southwestern corner) is not differentiated in the hypothetical map from the larger Canyonlands area of Subtropical Lower Montane Desert Scrub.

Interestingly, the woody plant, mammal,
reptile, and amphibian data (Figs. 6, 7, 8) suggest no absolute differences, but rather a gradual diminution of species numbers in the case of animals and replacement of shrub species. This is not to say that the use of animal and plant species distributions cannot be used to delimit the Mojave desert. MacMahon (1977b) defines boundaries of all North American deserts based on exactly such data.

Fig. 8. Distribution limits of reptiles and amphibians in Utah based on Stebbins (1966). A-boundaries of amphibians. B-boundaries of lizards. C-boundaries of snakes. D-analysis of the percentage of the entire Utah herpetofauna occurring in any one area. Analysis based on a grid of 10 x 10 mi (16 x 16 km) cells.
The point is that one must pick certain species as indicators to rigidly define the Mojave desert, but an analysis of the distributions of all species in the desert communities shows gradual loss or replacement over a broader area. The same is true for the Great Basin desert. The gradual species shifts and assignment of indicators is detailed in MacMahon (1977b).

The Holdridge scheme separates the Great Basin desert from the other semiarid areas of the state by segregating western Utah into Subtropical Montane Desert Scrub plus Subtropical Montane Steppe. We believe this differentiation is probably important, because western Utah communities subjectively appear to us to be quite different from those of the southeast corner despite floral overlap. Thus the vegetation map implies a higher degree of similarity than we believe exists, particularly for management purposes. Again, animal boundaries (Figs. 7, 8) are strongly coincident with separation of the Canyonlands area from the western deserts.

All data suggest that the Holdridge scheme effectively predicts plant- and animal-based life zone boundaries, if one can ignore a few “indicator” species. These data reinforce the general findings of others mentioned previously that the Holdridge scheme shows promise, but are more persuasive in that they use plants and animals in a topographically complex area where distributions are well known.

An interesting offshoot of these analyses are shown in Figures 9 and 10. It is usually assumed that long-term weather records would be necessary to derive Holdridge’s climatic variables. Our data suggest, for Utah, that mean annual biotemperature can be predicted from mean annual temperature (Fig. 9). This is not surprising, but it means that one can take mean annual temperature data from a weather station in a valley corrected for altitude, etc., to get a corrected mean annual temperature for a place distant from that station. Mean biotemperature may be read directly from the curve or calculated from the formulae. Additionally, for Utah sites, a single measurement of snow accumulation on one day a year (1 April, Snow Water Equivalents) predicts annual precipitation (Fig. 10). For Utah this high

**Fig. 9.** Relationship between mean annual biotemperature and mean annual temperature for Utah weather stations.

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\begin{align*}
Y (°C) & = 8.8186 - 0.5048X - 0.0578X^2 \\
Y (°F) & = 60.5685 - 1.0416X - 0.0132X^2 \\
R^2 & = 0.99
\end{align*}
\]

**Fig. 10.** Relationship between the 1 April snow water equivalent (SWE) and the annual precipitation for localities in the Manti-LaSal National Forest having snow courses studied by the United States Soil Conservation Service.
correlation is due in part to the high percentage of precipitation (60 percent or more) that comes as snowfall. A similar relationship may be of no value in other areas, but these results suggest that a person might be able to develop various other corrections specific to particular geographic areas. The prospect of using simple data extends the potential use of the Holdridge scheme. Additionally, since one only needs values for two variables to assign an area to a life zone hexagon, one may actually read the approximate value of the unknown third parameter off of the life zone model (Thompson 1966).

The Holdridge life zone model does predict plant and animal aggregations for Utah with reasonable accuracy. The next step to reach the final goal of using this scheme to portion the earth into a reasonable number of subsections for management purposes is to apply the scheme to another area containing organisms not closely related to those of Utah and then to determine whether or not a similar value of C obtains for the unrelated areas falling into the same life zone. That analysis must be left for another place and time.

ACKNOWLEDGMENTS

This work was made possible by the US/IBP Desert Biome funded by the National Science Foundation (Grant GB32139). Donna Baranowski and Bette Peitersen aided in manuscript preparation, and Linda Finchum typed the manuscript. The United States Forest Service, Dixie National Forest, and Soil Conservation Service, Manti-LaSal Snow Course Project, kindly permitted use of their data.

LITERATURE CITED


