Environmental Management (2014) 54:1249–1266
DOI 10.1007/s00267-014-0364-1

PROFILE

Ecoregions of the Conterminous United States: Evolution of a Hierarchical Spatial Framework

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Received: 21 March 2014 / Accepted: 26 August 2014 / Published online: 16 September 2014
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Abstract A map of ecological regions of the conterminous United States, first published in 1987, has been greatly refined and expanded into a hierarchical spatial framework in response to user needs, particularly by state resource management agencies. In collaboration with scientists and resource managers from numerous agencies and institutions in the United States, Mexico, and Canada, the framework has been expanded to cover North America, and the original ecoregions (now termed Level III) have been refined, subdivided, and aggregated to identify coarser as well as more detailed spatial units. The most generalized units (Level I) define 10 ecoregions in the conterminous U.S., while the finest-scale units (Level IV) identify 967 ecoregions. In this paper, we explain the logic underpinning the approach, discuss the evolution of the regional mapping process, and provide examples of how the ecoregions were distinguished at each hierarchical level. The variety of applications of the ecoregion framework illustrates its utility in resource assessment and management.

Keywords Ecoregions · Spatial frameworks · Ecosystem management · Regionalization · United States · North America

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Introduction

Debate over the magnitude of environmental degradation is increasing. Although many will argue the meanings of quality, health, and integrity as they pertain to ecosystems and environmental resources, most people would agree that the present conditions of these resources are not what they were before Europeans set foot on the North American continent, and that the changes are increasing with time. Moreover, it is apparent that the changes are occurring differently in different regions for different reasons (e.g., Drummond and Loveland 2010; Sleeter et al. 2011, 2012; Auch et al. 2011). Wise decisions regarding the management of environmental resources are dependent on knowing (1) the regionalities of characteristics of environmental resources, (2) how much these resources have changed, (3) the regional differences in the changes, and (4) the factors causing or associated with the changes. The problem is, of course, complicated by political and economic considerations regarding the values of ecosystems and environmental resources (Daily 1997). Orr (2012) elevated the issue to one critical to our national security stating: "A larger vision of security includes the internal resilience, health, and sustainability of the nation." Because the resilience and sustainability of ecosystems and environmental resources vary regionally, we cannot make effective assessment and management decisions without understanding these regional differences and without using a geographic framework that recognizes them at multiple scales or levels of detail (e.g., continental, national, and various levels of regional detail).

In 1987, the first map of what are now known as Level III ecoregions of the conterminous United States was published in the Annals of the Association of American Geographers (Omernik 1987). Initially intended to provide

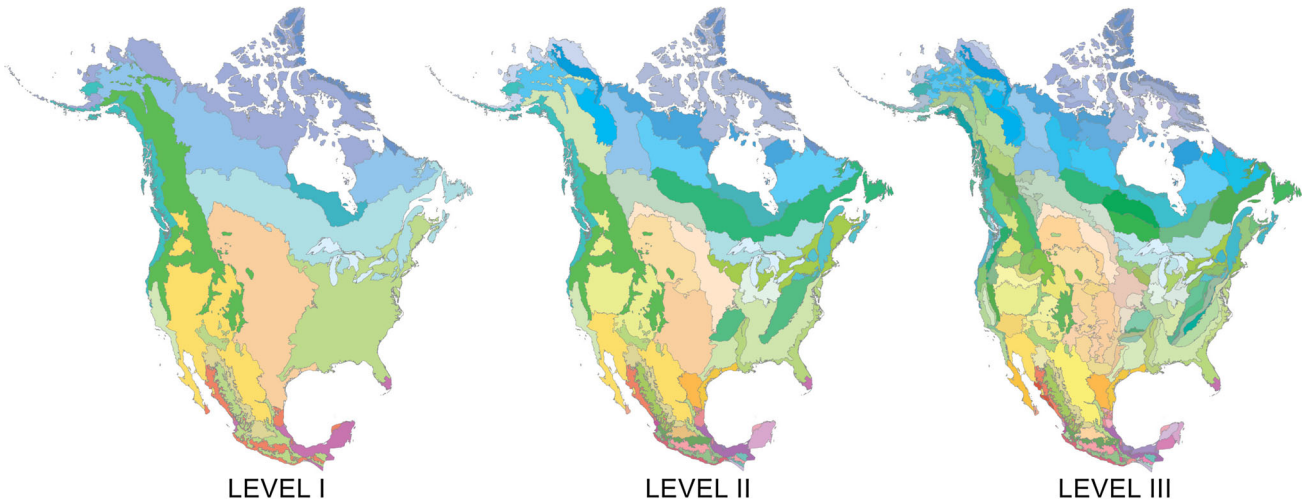

Fig. 1 Level I, II, and III ecological regions of North America. The names and identification numbers of these ecoregions are given in CEC 1997 and 2006. These maps and others of all four levels of ecoregions of the United State are available at www.epa.gov/wed/pages/ecoregions.htm

a geographic framework for managing aquatic resources, the purpose evolved into one of facilitating ecosystem management and environmental understanding in the broadest sense of the term, encompassing the abiotic and biotic components of terrestrial as well as aquatic ecosystems, with humans being considered as part of the biota. This evolution occurred because of the way the regions were defined which required considering the mosaic of all geographic phenomena that result in spatial differences in the quality and quantity of water.

Although the basic approach for defining these ecoregions has not changed substantially since the publication of the 1987 map, the scale and tools of mapping, amount of data, and involvement of local expertise all increased as the framework was refined and expanded. In collaboration with resource managers and scientists from many agencies and institutions in the United States, Canada and Mexico, the mapping has been expanded into the rest of North America (CEC 1997), the original Level III regions have been refined and subdivided into Level IV regions, and broader-scale Level I and II regions have been delineated (Fig. 1). In this paper, we explain how the process for developing this ecoregion framework has evolved since the 1987 map was published. We also enlarge upon the approach by providing examples of how the ecoregions were distinguished at each hierarchical level and how this varied from one part of the country to another.

The Nature of Ecoregions and Disagreement over How to Define Them

In the paper accompanying the 1987 map it was noted that "…there is little disagreement or misunderstanding about the meaning of *ecoregion*," (Omernik 1987, p. 123). However, since then, as interest in ecoregions and their applications rapidly grew (Loveland and Merchant 2004), so did the disagreement over their meaning and particularly over how they should be defined. This was probably due to the fact that many, if not most, of the agencies and programs that became interested in ecosystem management had a history of managing specific aspects or components of ecosystems (e.g., forestry, agricultural potential, biodiversity, and conservation of endangered species) and had developed or were using geographic frameworks designed for those specific purposes. The U.S. General Accounting Office, now called the U.S. Government Accountability Office (GAO), noticed this problem and requested that federal resource management agencies become more coordinated in their activities by developing a common geographical framework to address entire ecological systems (U.S. GAO 1994).

While there had been an informal group of federal agency personnel that had been meeting to discuss interagency ecoregion mapping in about 1993, the 1994 GAO report added momentum to the formation of a National Interagency Technical Team (NITT), representing the major resource management agencies, and tasked to develop a framework of common ecological regions. Although it was apparent to some that the existing natural-resource spatial frameworks had been developed by different individuals or groups from different agencies having different missions, and by different methods [e.g., Ecological Subregions by the U.S. Forest Service (USFS) (Bailey et al. 1994; Cleland et al. 2007), Major Land Resource Regions by the Natural Resources Conservation Service (NRCS) (U.S. Department of Agriculture-NRCS 2006), and ecoregions by the U.S. Environmental Protection Agency (EPA)], there was an initial

reluctance by others to recognize these differences and the need for a framework that addressed the broader needs of ecosystem management that crossed more specific individual agency interests. This was understandable because many if not most of the agency representatives had invested considerable time and effort in developing their respective frameworks and/or had natural biases toward specific aspects of ecosystems (e.g., soils, vegetation, geology, hydrology, and land use) because of their backgrounds or agency affiliations. However, after multiple meetings over several years, the NITT finally agreed on a goal of developing a framework that addressed regional similarities in the mosaic of biotic, abiotic, terrestrial, and aquatic ecosystem components with humans being considered as part of the biota. The team then examined the existing frameworks and maps of combinations of geographic characteristics associated with differences in ecosystems and agreed on an approximation of one level of ecological regions (McMahon et al. 2001). In spite of the apparent success of the NITT, disagreement remained regarding the nature of ecological regions and how they should be defined (e.g., Olstad 2012). In one of the papers in a special issue of Environmental Management on "Ecoregions for Environmental Management," McMahon et al. (2004) stated: "Despite the wide use of ecological regions in conservation and resource management evaluations and assessments, a commonly accepted theoretical basis for ecoregionalization does not exist."

Besides investment in existing frameworks, reluctance to change, and bias toward a single characteristic, several other reasons for disagreement over how to delineate ecoregions have been noted (Omernik 2004). They include disagreement over the definition of ecosystems and ecoregions, ecoregion boundary complexity, and whether to use quantitative (rule based) or qualitative (weight-of-evidence) approaches. The lack of agreement on and the evolving nature of the definition of "ecosystems" complicated reaching consensus on the delineation of ecological regions. Agreeing on appropriate methods to define ecoregions is difficult enough, but even more so if there is little agreement on the subject, ecosystems, that people are attempting to regionalize. Ecosystem is a contested term with many definitions (Gonzalez 1996; Jax 2006; Haber 2011) and these appear to have evolved from centering more on the biota, to subsuming biotic and abiotic characteristics but in the absence of humans, to definitions that consider humans as part of the biota (Willis 1997; Corn 1993; Sheifer 1996; Callicott 1994; Allen and Hoekstra 1994; Likens 1993; Christensen et al. 1996).

Much of the disagreement on the definition of ecosystems is the result of their complexity and a reluctance to recognize the inevitable subjective criteria necessary for deciding on the scale, extent, and hierarchy of ecosystems, which runs counter to the traditional scientific method (Kay and Schneider 1994). As there is no observer-independent way of defining ecosystems, the concept itself has been questioned (Kay and Schneider 1994; Callicott 1995; Fitzsimmons 1996; Lackey 1999), and debates occur over whether ecosystems are abstract concepts or areas with geographical borders (Marin 1997; Rowe 1997; Blew 1996; Rowe and Barnes 1994). The argument, however, does not seem to be simply one of bio-ecologists centering their ecosystems on organisms versus geo-ecologists centering their ecosystem on geographic spaces, as Rowe and Barnes (1994) have implied. Differences in perceptions of ecosystems, which are often associated with uses (Gonzalez 1996), seem to be infinite, as are the spatial and temporal variations of the quality and quantity of environmental resources and interrelations of ecosystem components.

While recognizing the merits of academic and epistemological debates about ecosystems, working with applied scientists and resource management agencies often leads to development of tools that exhibit some degrees of usefulness in resource research, monitoring, and assessment. Many scientists, resource managers, and land owners are ultimately interested in the areas or regions within which the mosaic of all biotic and abiotic ecosystem components is different or exhibits certain patterns. Because ecosystems are far too complex for us to comprehend completely, we have no choice but to simplify our understanding of the world around us with maps, models, and classifications that can offer some insight and utility. Regionalization, a specialized form of classification, has a rich history in the geographic sciences (Hartshorne 1939; Hart 1982), while ecology brings a different perspective to the task (Bailey 1996; Loveland and Merchant 2004). That task is to somehow view and interpret the patterns of as many factors as possible that cause or reflect spatial differences in ecosystems and to delineate areas of similarity.

Although the debate about the advantages of quantitative or qualitative approaches to define regions has been discussed in several papers (e.g., Loveland and Merchant 2004; McMahon et al. 2004; Hargrove and Hoffman 2004; Omernik 2004), an important misconception remains concerning the replicability of approaches termed quantitative, rule based, or systematic. Many who espouse quantitative approaches claim that they are repeatable and therefore more defensible than a qualitative method that is based on human expertise (e.g., Hargrove and Hoffman 2004). While acknowledging this common belief, a number of reviewers of ecoregion mapping approaches have cautioned that this thinking may be flawed in that subjectivity was in fact involved in the development of all of these frameworks (Loveland and Merchant 2004; Olstad 2012; McMahon et al. 2004). Neither the systematic approaches that are primarily statistical and geographic information

systems (GIS) based (e.g., Hargrove and Hoffman 2004) nor those based on assumptions about the importance of single geographical phenomena acting as a controlling factor relative to each hierarchical level of regionalization (e.g., Bailey 1983) are completely objective. In the case of statistical and GIS-based approaches, judgments are made in determining which geographic characteristics, classifications, and mapped representations of those characteristics are used in the regionalization process and how each characteristic will be treated statistically. Also, to compile frameworks using broader systematic approaches, such as that of Robert Bailey, subjective decisions must be made in interpreting each of the *underlying principles* and the various associated caveats (Bailey 2004).

In order for a mapping method to be truly replicable, an independent person or group must be able to reproduce the map using only documentation of the method but not the final product of the original. This might be possible for a method such as that of Hargrove and Hoffman (2004), *if* the step by step process were made more explicit, such that the person or groups reproducing the map would be able to perform the work in a completely mechanistic manner. At present, that type of documentation is not available for any of the ecoregion frameworks. But of greater importance is the defensibility of the approach. We question the assumption that an ecoregion map produced using a quantitative approach is more defensible than one using a holistic/weight-of-evidence approach. The defensibility of an ecoregion framework should be judged by its *usefulness* rather than how it was developed. This, of course, is problematic if usefulness is tested by only one or two variables, which is generally not appropriate for ecoregions. Whereas a special or single purpose map, such as one of soils, physiography, vegetation, or a water-quality characteristic can be tested against patterns of independently collected data on that characteristic, ecological regions represent areas within which there is relative similarity in the mosaic of all ecosystem components—biotic, abiotic, terrestrial, and aquatic, with humans being part of the biota. The factors associated with regional differences in ecosystems are interrelated in an infinite number of ways spatially and temporally. For research and assessment projects that analyze subjects that reflect interactions of many geographical and ecosystem characteristics, ecoregion frameworks developed using a qualitative, weight-of-evidence approach have proven to be effective. Examples of these applications are discussed later.

The reasons for disagreement over how to define ecoregions are of course interrelated. During field verification of a draft version of Level III and IV ecoregions of Kentucky (Woods et al. 2002), a group of scientists and resource managers representing different disciplines met with an ecologist/botanist to get his thoughts on the draft map. In his response, he noted that he preferred a map he had prepared for The Nature Conservancy (TNC) (Campbell 1996) saying: "I have emphasized vegetation and plant distributions, which I think is useful, and gives my map an edge over others that claim to be biogeographic, but do not really take details into consideration." He then went on to say, "Actually, my main conclusion is that there is no perfect eco/regional map—there are too many viewpoints, applications, and biases to allow a perfect map." (Julian Campbell, 2000, personal communication). While Campbell's map may be well-suited for the purposes of TNC, his comments reflect the interrelatedness of the reasons for disagreement over how to define ecoregions, particularly the disagreement over the term *ecosystems*, the complexity of the nature of ecoregions and ecoregion boundaries, and our natural bias toward particular characteristics. Campbell's concluding comment illustrates the difficulty, or inability, for some to see the whole (the entirety of ecosystems) for the parts, which may in turn reflect perspectives influenced by different backgrounds or intellectual or institutional investments in one or more specific ecosystem parts.

The crux of the problem centers on identifying *ecological regions* versus regions that focus on specific aspects of ecosystems (e.g., areas of unique biodiversity, fish distributions, or agricultural potential). Ecoregions should depict areas of similarity in the collective patterns of all biotic, abiotic, terrestrial, and aquatic ecosystem components with humans being part of the biota. As such, these regions are most useful for integrating resource assessment and management strategies across agencies and programs that have different missions for the same geographical areas if their interests are on entire ecosystems. For narrower purposes, frameworks tailored for those uses may be more helpful. The identification of a hierarchical framework of ecological regions would appear to be essential, however, for a better understanding of the resilience, health, and sustainability of ecosystems and natural resources, an understanding that Orr (2012) suggested is necessary to our natural security.

In his popular book "Collapse: How Societies Choose to Fail or Succeed" Diamond (2005) examined the complexities, regionalities, and consequences of human interactions with the environment and commented:

> *"People often ask, 'What is the single most important environmental/population problem facing the world today?' A flip answer would be, 'the single most important problem is our misguided focus on identifying the single most important problem!' That flip answer is essentially correct, because any of the dozen problems if unsolved would do us grave harm, and because they all interact with each other."* (Diamond 2005, p 498).

It therefore follows that to adequately define and understand ecoregions, much less apply them to environmental management, one must recognize the interrelatedness of natural capacities of the environment and human activities (Bryce et al. 1999). Although these interrelationships vary infinitely in space and time, they exhibit distinguishable regional patterns at all levels of detail (as Diamond points out in his book), from coarse continental scales to regional and local scales. Hence, the need to define a hierarchical framework of ecological regions that captures these particular patterns in the capacities of ecosystems and environmental resources and their resiliencies and tolerances to human impacts is obvious.

Approach

Our approach to define ecoregions is one of pattern analysis. It incorporates the spatial correlation of both physical and biological factors. The combination of factors associated with spatial differences in ecosystems must be visualized from a distance that allows distinction of patterns in the mosaic of ecosystem components from individual associations. If one examines a pointillist-type painting, such as those of Seurat, too closely using a magnifying glass, only different-colored dots are distinguishable. To construct the picture by attempting to understand how each differently colored dot is related with adjacent dots is futile. Only by standing back away from the painting can the meaningful patterns of dots be seen sufficiently to visualize the subject. The same is true with ecological regions, but in the case of ecoregions, the *pictures* can be perceived at various hierarchical levels. If the combinations of geographic phenomena associated with spatial differences in ecosystems are viewed at a continental scale, it becomes apparent that the capacities and resiliencies of similar-sized regions with similar types of geographic characteristics, say Australia and the conterminous United States, are strikingly different. Both of these areas contain regions ranging from deserts to moist highland forests, but the distributions, mosaics, and quantity and quality of environmental resources are dramatically different, particularly regarding soil and forest productivity, geologic history, and climate (Diamond 2005). Even regions of the world with similar apparent capacities, such as the wheat and corn/maize regions, are in fact dissimilar because of differences in geologic and anthropogenic histories.

The number and relative importance of factors associated with spatial differences in ecological regions vary from one region to another regardless of the scale or hierarchical level of regionalization (Wiken 1986, Omernik 1987, 2004). When viewing North America or the conterminous United States from a coarse level, the Great Plains are easily distinguished from the Eastern Temperate Forests and the Northwestern Forested Mountains; the Great Plains being relatively flat, relatively dry, originally mostly grass-covered and now predominately agricultural compared to the more mesic originally forest-covered region of plains, hills, and low mountains to the east, and higher mountains in the west that are characterized by elevational banding. These broad ecological regions have been categorized as Level I (CEC 1997, Omernik 2004, www.epa.gov/wed/pages/ecoregions/na_eco.htm). A portion of the Great Plains Level I ecoregion as well as the Level II and III ecoregions nested within it are shown in Fig. 2.

Although easily distinguished from one another in a broad sense, each of the Level I ecoregions contains considerable variability, much of which is reduced by identifying more detailed Level II ecoregions nested within the Level I regions. For example, within the Great Plains, the West-Central Semi-Arid Prairies are drier and contain less cropland agriculture than the Temperate Plains to the east and are cooler than the South-Central Semi-Arid Prairies to the south. The mosaics of potential natural vegetation and current land use/land cover are markedly different in each of these regions. In contrast to the Temperate Plains and West-Central Semi-Arid Prairies where corn, soybeans, spring wheat, and barley are major crops, in the South-Central Semi-Arid Prairies, winter wheat, sorghum and, locally, cotton are dominant, reflecting a difference in phenology between the regions.

The variability within Level II ecoregions is further reduced through identification of the more detailed Level III ecoregions. As with the coarser levels, at Level III, the relative importance of each of the combination of geographic characteristics that distinguish each ecoregion also varies from region to region as does the relative homogeneity and heterogeneity of each region. The Flint Hills (28), Nebraska Sand Hills (44), and, to a lesser extent, the Edwards Plateau (30) are all examples of relatively homogeneous regions compared to the complex Southwest Tablelands (26) that comprised a mosaic of canyons, mesas, badlands, and dissected river breaks with some scattered flat to rolling areas of cropland (Fig. 2). In contrast to the Southwest Tablelands, the bordering High Plains (25) mostly consist of smooth to slightly irregular plains having a higher percentage of cropland agriculture, but also contain scattered rolling sand plains, sand hills, and dunes. Whereas the variability in many Level III ecoregions in the Great Plains is largely explained by differences in a combination of soils, physiography, potential natural vegetation, and land use characteristics, variability in the Nebraska Sand Hills is associated primarily with differences in hydrologic characteristics. These differences, while not as contrasting as in many other Level III ecoregions, are sufficiently important to justify delineation of

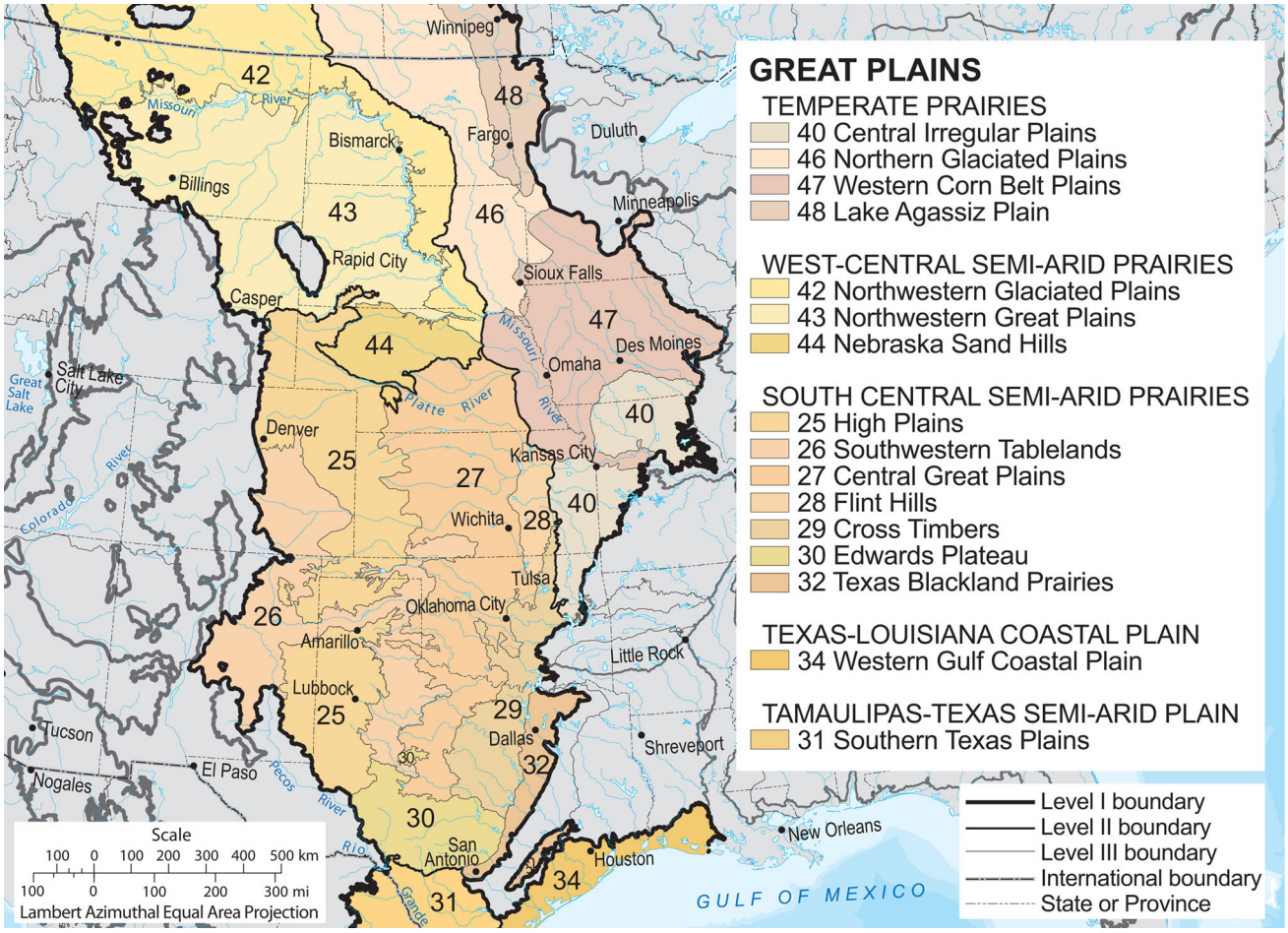

Fig. 2 Level II and III ecoregions of a portion of the Great Plains

Level IV ecoregions within the Nebraska Sand Hills. Much of the ecoregion contains streams but no lakes, while other portions are mostly devoid of streams and contain many lakes with groundwater interaction, and one area contains alkaline lakes that are largely perched and have limited influence with groundwater (Fig. 3).

The way in which Level IV ecoregions are distinguished within Level III is different and strikingly more complex in the North American Deserts of the Western United States (much of which is commonly called the Basin and Range) than in the Great Plains. The Northern Basin and Range (80), Central Basin and Range (13), Mojave Basin and Range (14), and Sonoran Basin and Range (81) Level III ecoregions each contain a different mosaic of dry basins and ranges (Fig. 4). Each exhibits a unique pattern of physiographic, geologic, pedologic, botanic, hydrologic, and climatic characteristics. For example, the Northern Basin and Range contains fewer mountain ranges than the Central Basin and Range and is underlain by mostly volcanic rocks compared to the mix of sedimentary and volcanic rocks in the Central Basin and Range. The pattern of potential natural vegetation in the cooler Northern Basin and Range is mostly sagebrush steppe in contrast to a pattern of predominantly saltbush–greasewood, Great Basin sagebrush, with patches of juniper-pinyon woodland and even some ponderosa pine and conifer forest at higher elevations, in the Central Basin and Range. The close proximity of the mountain ranges in the Central Basin and Range compared to the relative paucity of higher ranges in the Northern Basin and Range also influences the patterns of wildlife in the two regions (Trimble 1989; Wildlife Action Plan Team 2012). Although the combination of characteristics that distinguish each of these regions is quite different, the spatial extent of each of the characteristics (e.g., soils, physiography, geology, and vegetation) that predominate in the Northern Basin and Range is not the same as that of the Central Basin and Range. That is, if one were to base the boundary between the two Level III regions on soils, it would not be the same as if the boundary were based on physiography, and neither of these boundaries would be the same if the basis were differences in vegetation (Omernik 2004). Hence, there is a certain

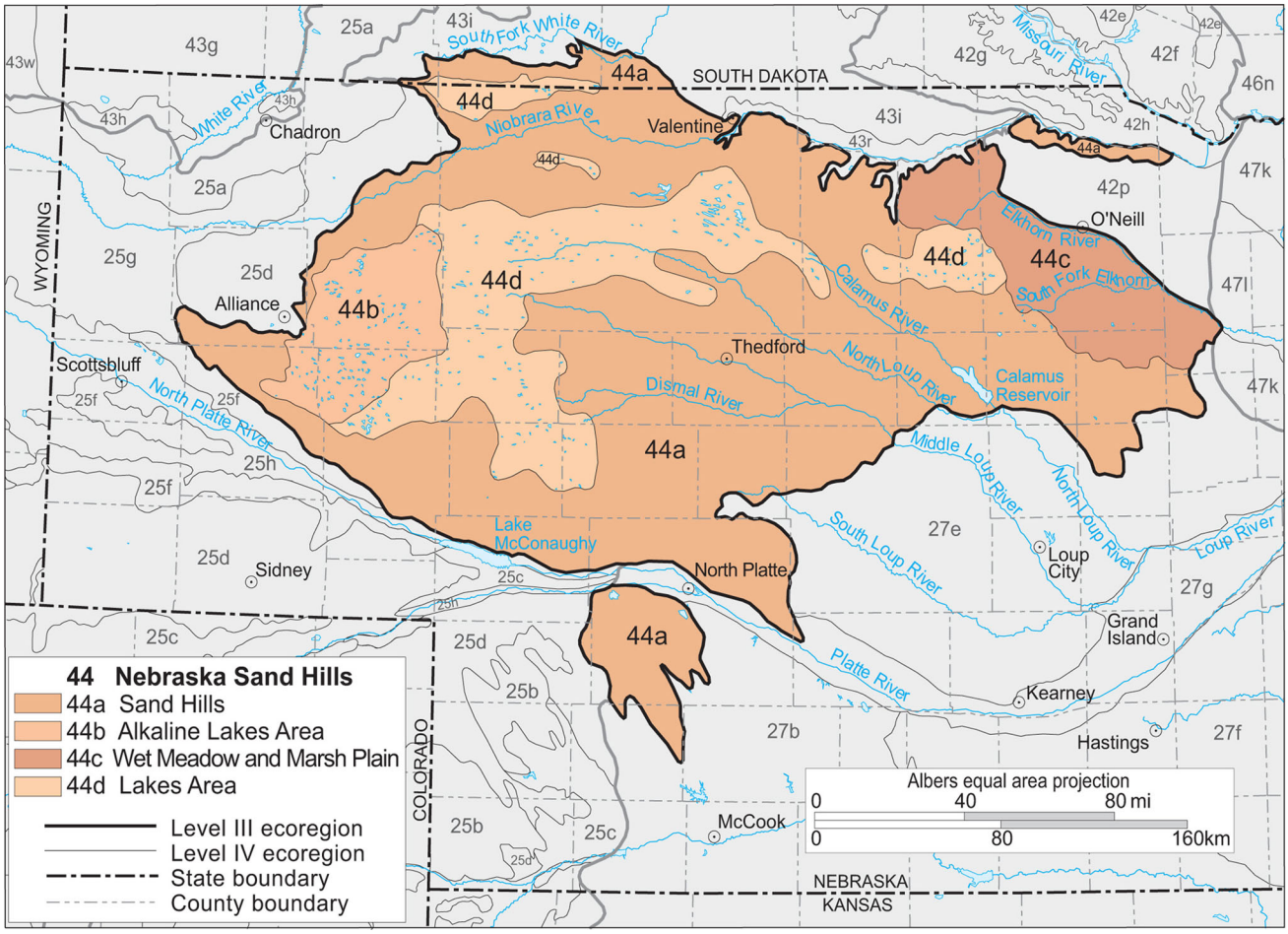

Fig. 3 Level III and IV ecoregions of the Nebraska Sand Hills

amount of fuzziness to ecoregion boundaries such that Level IV regions do not fit perfectly within Level III regions, although for cartographic and database purposes, we force such a fit. This level of generality varies from one hierarchical level to another as well as from region to region. For example, entire Level III ecoregions occur within the fuzzy boundary between the Great Plains and Eastern Temperate Forest Level I ecoregions (Omernik 2004). Some boundaries such as those of the Nebraska Sand Hills and the eastern side of the Edwards Plateau are relatively precise. Other boundaries such as that between the Edwards Plateau and the Chihuahuan Deserts are imprecise reflecting gradual changes in primary distinguishing characteristics between adjacent regions. In some of the earlier ecoregion mapping projects, in States such as Alabama, Iowa, Massachusetts, Mississippi, and Oregon, efforts were made to map boundary transition widths and provide other information about the nature of the ecoregion boundaries (e.g., Clarke et al. 1991; Griffith et al. 1994a, b). These efforts were not entirely satisfactory in communicating the varied complexity of ecoregion boundary delineations in different parts of the country, or for convincing users that boundaries are perhaps better viewed as areas, rather than lines, where the predominate characteristics of one region meet the predominate characteristics of another region (Omernik 2004).

Subdividing the Level III ecological regions of the North American Deserts (such as in the Central Basin and Range) involved distinguishing the elevational bands that contained substantial differences in terrestrial, aquatic, and biotic and abiotic ecosystem components as well as delineating the regions within which these bands, or patterns in the bands, differed because of geologic, hydrologic, and climatic influences. For example, the elevational bands within the carbonate basins and ranges are markedly different than those of the volcanic basins and ranges to the west and both are dissimilar to those of the Tonopah region to the south. While not defining ecological regions per se, in his book "The Sagebrush Ocean," Trimble (1989) recognized both of these types of regions within the Central Basin and Range. In the Northern Basin and Range, the Level IV ecoregions with internal drainage are

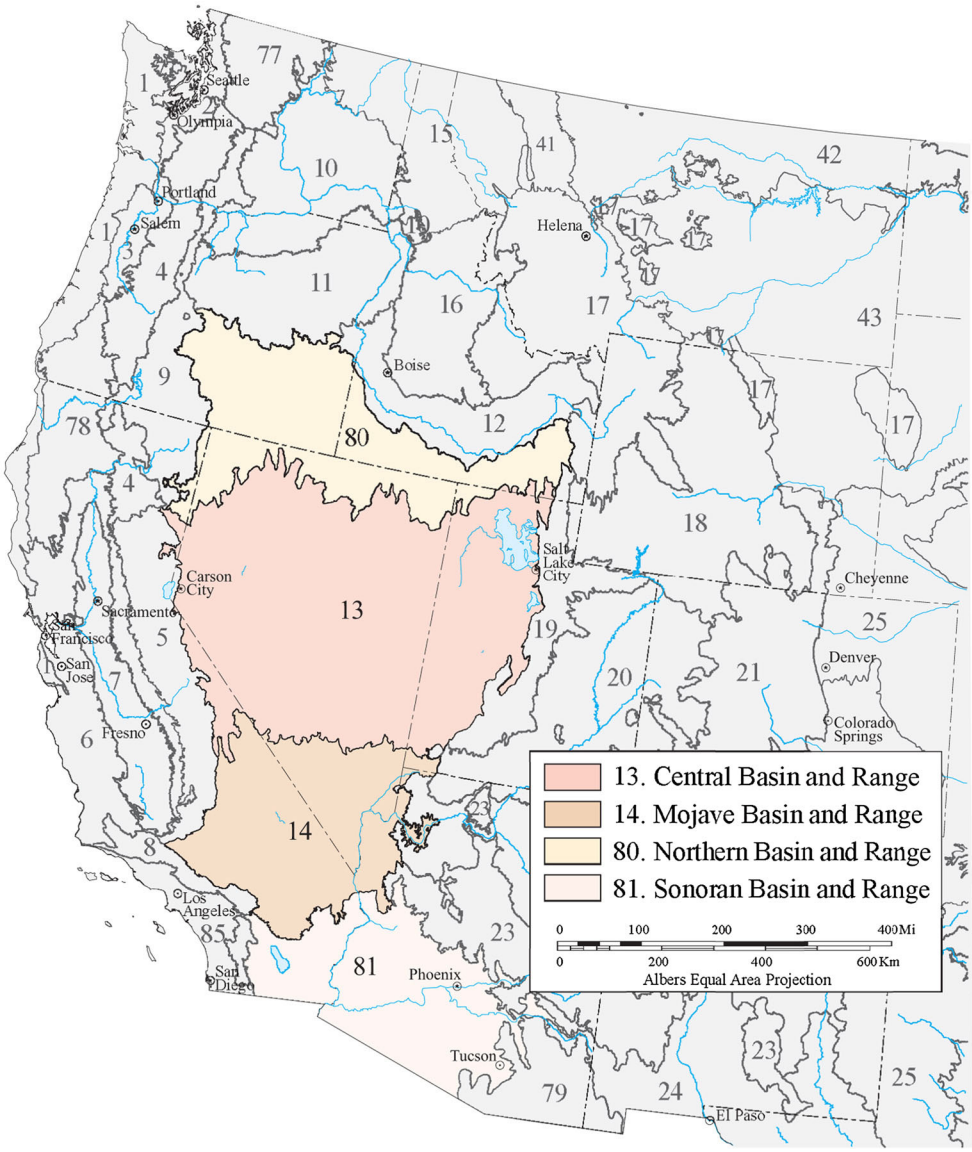

Fig. 4 Selected Level III ecoregions of the Basin and Range, Western United States

distinguished from those that drain to the Snake River, and these are differentiated from the wooded uplands and partly forested mountains (Fig. 5). Thus, the relative importance of the primary distinguishing characteristics of each ecoregion varies from one ecoregion to another at all hierarchical levels (I, II, III, and IV).

In many state projects, questions arose concerning human impacts and, specifically, the idea of urban ecosystems and the complicated relationship of large urban expanses and ecoregions. Do large cities or expanses of megalopolis constitute their own ecoregion? Are cities in different parts of the country more similar to each other than with the ecoregion in which they are located? Although the science and understanding of urban forms are increasing, including scientific journals devoted to urban ecosystems, these are difficult questions, and recent data provide mixed answers to the similarities and differences of cities depending on which parameters are examined (e.g., Coles et al. 2012; Groffman et al. 2014; Terzioti and McMahon 2012). Obviously, human impacts are ubiquitous (Vitousek et al. 1997; Sanderson et al. 2002; Hook et al. 2012). With "nature" so embedded within human-shaped mosaics of land use and land cover, some have defined anthropogenic biomes to illustrate this intermingling of human and natural systems (Ellis and Ramankutty 2008). It is not just a question of urban versus non-urban areas, as land use dynamics in exurban and rural areas affect such large areas and have profound ecological effects (Theobold 2005; Brown et al. 2005). There is a continuum of human uses and influences in all of the

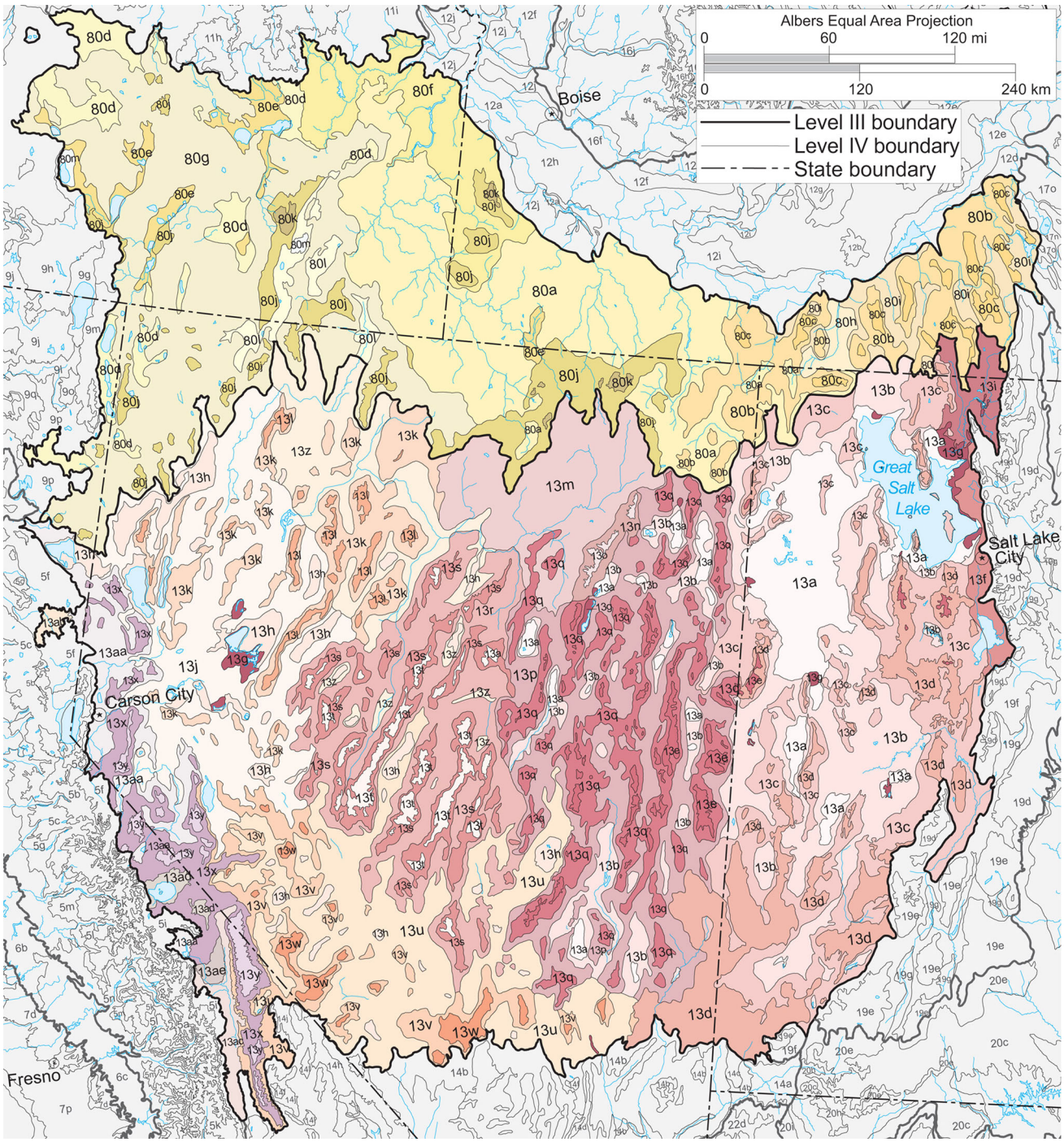

Fig. 5 Level IV ecoregions of the Northern Basin and Range (Level III #80) and Central Basin and Range (Level III #13)

ecoregions, from nearly total urban, to suburban, exurban, agricultural, rangeland, a variety of forested lands, to "wild" land, among other uses. Some of the Level IV ecoregions are dominated by developed land cover, e.g., the Portland/Vancouver Basin (3a), San Francisco Peninsula (6s), Bay Terraces/Lower Santa Clara Valley (6t), Chicago Lake Plain (54b), Boston Basin (59d), Miami Ridge/Atlantic Coastal Strip (76c), and Los Angeles Plain (85d), or by a combination of urban/suburban/exurban and irrigated cropland land covers and highly altered hydrology such as around Phoenix in the Gila/Salt Intermediate Basins (81n). These are essentially urban ecoregions, but in these examples, there were generally strong physical or ecological characteristics that helped define the ecoregions. With the general evidence that city characteristics are influenced by their regional context, most other large urban

areas were mapped as part of the human-influenced ecological mosaic of larger-area ecoregions.

The Process

The first approximation of ecoregions of the conterminous United States mapped by Omernik (1987) depicted 76 of what are now termed Level III ecoregions. The map was developed at a relatively small scale (1:3,168,000) and published at an even smaller 1:7,500,000 scale (Omernik 1987, 1995). Much of the mapped information on geographic characteristics (including soils, physiography, vegetation, land use, geology, and hydrology) used to delineate these ecoregions was from 1:7,500,000 scale maps, many of which were part of the U.S. Geological Survey (USGS) National Atlas (USGS), although larger and smaller scale maps from a number of other sources were also consulted (Omernik 1987, 1995). As applications of the framework increased, particularly at the state level (e.g., U.S. EPA 1986; Fandrei et al. 1986; Heiskary and Wilson 1989; Larsen et al. 1988), interest in refining and subdividing the framework also grew. Working with their assigned states, some EPA Regional offices, most notably Regions 4 (Southeast) and 7 (Central Midwest), initiated projects with the EPA research laboratory in Corvallis, Oregon [now the Western Ecology Division of EPA's Office of Research and Development (EPA-WED)] to further develop the framework in states that expressed the greatest interest in applying ecoregions (e.g., Griffith et al. 1994). These projects precipitated similar collaborative projects in other states and EPA Regions, and as the associated learning curve advanced, the steps for conducting state ecoregion mapping in a consistent manner soon became established.

Because the development of the Level IV framework was conducted at a far greater level of detail than that of the 1987 map and involved collaboration with resource managers and experts in many aspects of ecosystems, the work involved more than an order of magnitude more time and effort than that of the initial Level III mapping. The delineation of the Level IV ecoregions was conducted at the 1:250,000 scale and involved more extensive research on historical ecological change as well as current conditions. The duration of each state-level project, from the information-gathering stage to the point where the final descriptions and map were ready for review and subsequent publication, varied from one and a half to three years. It should also be noted that during the period of Level IV ecoregion mapping, from the early 1990s to 2012, there was a continuing revolution in mapping and computer technology, remote sensing, and the development and availability of Earth science databases (DiBiase et al. 2006; Longley et al. 2011). Although the ecoregion mapping process was not a computational-heavy, automated, overlay or modeling approach, geographic information systems and the exponential growth of larger-scale and higher quality data were important parts in improving the basis and accuracy of the ecoregions and boundaries, the visualization of information, the quality of the cartographic products, and the efficiency of ecoregion data management.

With a few exceptions, the projects were conducted on a state-by-state basis, although always with a national perspective kept in mind. To decrease inconsistencies from one project to another, the work was facilitated by a small team of geographers at EPA–WED in Corvallis. At the start of each project, an introduction/information-gathering meeting was held in the state being mapped and was usually hosted by a state resource management agency or state office of a federal agency such as the Natural Resources Conservation Service (NRCS). People invited to these meetings included experts in aquatic and terrestrial ecosystems and factors associated with spatial differences in ecosystem health and integrity. These experts included soil scientists, geographers, geomorphologists, geologists, botanists, hydrologists, aquatic biologists, and wildlife zoologists, among other disciplines. Occasionally, questions from participants related to mapping rules and ideas such as sizes of minimum mapping units. The approach did not rely on a pre-determined set of rules that had been applied to all parts of the country, in contrast to methods used to develop some other frameworks. While the minimum size of regional units is influenced in part by the compilation scale of mapping, the importance and distinctiveness of small units were generally considered more meaningful than setting a strict numerical size limit. In a few instances, revisions were made to boundaries or classifications made for one state based on subsequent work in an adjacent state. Two or more review meetings were held throughout the course of each project. Participants at the review meetings included many of those who attended the initial introductory meeting, people who became coauthors or major collaborators, as well as by other researchers invited by attendees of the first meeting. Field examination was often conducted early in the project by the mapping geographers from EPA–WED, and, near the final draft stages, collaborative field verification trips were also conducted in 30 states. In some states, this additional collaborative field review was determined unnecessary by most of the participants, or for a few states, funding limitations, work schedule conflicts, or the unavailability of the needed cross-section of experts precluded this step.

Essential to the final uses of the ecoregion framework was the interaction of individuals from multiple agencies and with different areas of expertise in exploring, debating, and mapping patterns of ecological regions rather than

patterns of particular characteristics for specific purposes. Roundtable-type review sessions where attendees were able to listen and react to each other's comments helped enable this broader perspective. The field verification trips, designed to transect ecoregions and boundaries and further examine areas of disagreement, were particularly helpful in this regard. Although limited by scale (that is, not being able to stand far enough back from the subject to better perceive the whole for the parts), inspecting representative areas and listening to one another's comments among vehicles via two-way radios while crossing suggested boundaries were extremely useful in building consensus.

Although this approach for defining ecological regions stemmed from that of Omernik (1987) and has been termed the EPA approach, the logic underpinning it is basically the same as that of Wiken (1986), even though neither Wiken nor Omernik were aware of one another's work until after the initial ecoregion maps of Canada and the conterminous United States had been published. It is also important to note that the present hierarchical framework of ecoregions of the United States (www.epa.gov/wed/pages/ecoregions.htm) is the product of the efforts of over 600 individuals representing several federal agencies, many state agencies, and a number of non-government organizations (NGOs) and academic institutions. Federal agency representation in the mix of coauthors, collaborators, and contributors of the 26 published map/posters of Level III and IV ecoregions (seven of which covered two or more states) and other final products varied from one project to another. Of the over 130 coauthors, many represented the EPA, NRCS, USGS, and USFS. Involvement of multiple federal agencies in the refinement of Level III ecoregions and delineation of Level IV regions increased after the creation of the NITT effort to develop a common framework of ecological regions in the mid- to late-1990s. Although the EPA/state-level ecoregion projects were mostly independent of the NITT effort, the ultimate goals were the same, and the state projects often had representation and endorsement from the NITT.

Shortly before the NITT was conceived, the Commission for Environmental Cooperation (CEC) began a project to develop a framework of ecological regions for North America. Some of the major players in the initially EPA-led state-level projects and overall refinement and subdivision of the original 1987 ecoregion map were also members of the NITT and CEC activities. Hence, many of the modifications to the original 1987 map were the result of reexamining it in the process of developing the first levels of North American ecological regions and the common interagency framework for the U.S.

The use of Roman numerals to identify different hierarchical levels of ecological regions was also an outcome of the CEC mapping project. This scheme was chosen because of the confusion resulting from different agencies in different countries using different terms for the various hierarchical levels. Terms such as district, section, subsection, ecotone, domain, province, zone, and even ecoregion have been used. Most of these terms have more than one meaning and some refer to a different hierarchical level in one framework than that of another. The CEC group reasoned that regardless of the hierarchical level an ecological region is simply a *region.* At that point, the CEC framework and the EPA-led framework (that fit within the CEC Ecological Regions of North America) adopted the Roman numeral approach to identify hierarchical levels (CEC 1997). Subsequently, as the refinement of Level III ecoregions and definition of Level IV ecoregions progressed in the United States, a few revisions were made to Level III ecoregions adjacent to Canada and Mexico that were inconsistent with the Level I and II alignments on the CEC map published in 1997. To correct this inconsistency, and because the CEC also wanted to incorporate Level III ecological regions into the North American framework, the continental map was revised and made available in electronic form in 2006 (Wiken et al. 2011; US EPA 2013a).

There are several reasons for the dual coding schemes used for the CEC ecological regions and that of Level III and IV ecoregions of the conterminous United States. Before the CEC work involving participants from Canada, the United States, and Mexico began, the refinement and subdivision of Level III and IV ecoregions of the United States were already well underway, as were applications of the framework. Because most of the applications of ecoregions in the U.S. at the time the CEC effort began involved levels III and IV, and because the original version of ecoregions (Omernik 1987), now referred as Level III, was identified by numbers, lower case alphabetic identifiers were chosen for Level IV ecoregions (e.g., 42a, 42b, etc.) to best fit the needs of users. For many U.S. users of the ecoregion framework, the codes were too deeply ingrained in their work that a complete coding change would have been disruptive. On the other hand, for the CEC, using a scheme such as Roman numerals for one level, an upper case alphabetic identifier for the next, a number for the third, and a lower case alphabetic identifier for the fourth seemed too cumbersome, more so than the scheme that was ultimately chosen, which comprised numbers for each level separated by periods. So, for Level III, a user can use the U.S. code (e.g., 42 for the Northwestern Glaciated Plains) or the North American code (9.3.1).

For most of the EPA-led ecoregion mapping projects, the final maps and descriptions of the Level III and IV ecoregions were published in large format (36-inch × 46-inch) map/poster form. The state ecoregion map, descriptions of primary distinguishing characteristics of the ecoregions, as well as representative photos appear on the front side, and a summary table of ecoregion characteristics and

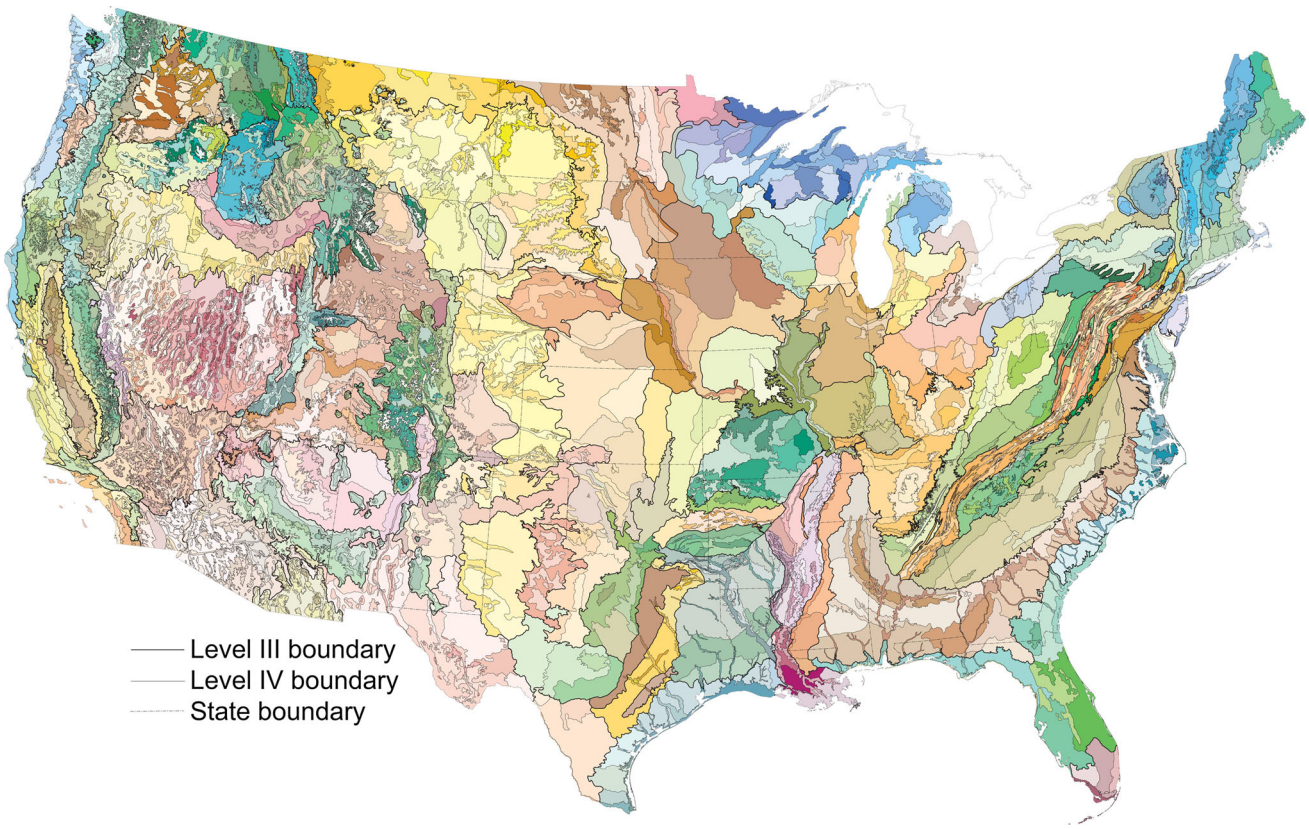

Fig. 6 Level III and IV ecoregions of the conterminous United States. Ecoregion names, descriptions, maps, and GIS data are available at www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm

a list of references are on the back. Thirty six of the conterminous United States are covered by these products. Besides these printed paper maps, digital versions of these posters, ecoregion maps of the remaining states, national maps, ecoregion descriptions, and GIS files are available at www.epa.gov/wed/pages/ecoregions.htm. Figure 6 illustrates the patterns and complexity of the 967 Level IV ecoregions of the conterminous United States.

Applications

The ultimate test of ecoregions is their usefulness. Albeit complex in nature, depicting spatial patterns in the mosaic of all ecosystem components, ecoregions are critical for environmental assessment, management and research activities that focus on multiple aspects of ecosystems. They are essential for integrating these activities across agencies and programs that have different interests in the same geographic areas as well as an overall interest in ecosystems as a whole. Because the quality and quantity of water at any point reflect the aggregate of geographic characteristics (both natural and anthropogenic) upgradient from that point and because ecoregions depict regional differences in this aggregate, the framework is particularly useful for integrating terrestrial- and aquatic-based research and assessment activities. Many regional, national, and continental level projects have found these ecoregions useful for applications that require consideration of this spatial interrelatedness (Table 1).

Most of the initial applications centered on structuring state- and regional-level water-quality assessment and regulatory programs. Many state resource management agencies have used ecoregions to develop biological criteria (e.g., Davis et al. 1996; Yoder and Rankin 1995; Hornig et al. 1995) while others (most notably Arkansas) have used the framework for setting water-quality standards (US EPA 1986; Rohm et al. 1987; Omernik and Griffith 1991). Minnesota has been using ecoregions for water-quality assessment and management since the mid-1980s. These applications have included making assessments of nonpoint source pollutants (Fandrei 1986; US EPA 1988), determining lake management goals (Heiskary and Wilson 1989; Heiskary and Lindon 2010), and developing nutrient criteria (Heiskary and Wilson 2008). Iowa, another State with a long history of ecoregion use beginning in 1986, used both Level III and IV ecoregions to locate sites for monitoring long-term trends in water

Table 1 A selected sample of state, federal, and other applications of EPA/USGS ecoregions

Institution	Ecoregion use	Reference
State agencies		
Arkansas	Level III ecoregions for setting dissolved oxygen water-quality standards. Level III and IV ecoregions for Comprehensive Wildlife Conservation Strategy	US EPA 1986; Omernik and Griffith 1991; Anderson 2006
Georgia	Level III and IV ecoregions to classify breeding bird occurrence, as framework for natural communities and Comprehensive Wildlife Conservation Strategy	Schneider et al. 2010; Edwards et al. 2012; Georgia DNR 2005
Iowa	Level III and IV ecoregions for reference site selection, long-term river monitoring trends	Griffith et al. 1994b; Iowa DNR 2001
Kentucky	Level III and IV ecoregions for Comprehensive Wildlife Conservation Strategy	Kentucky DFWR 2013
Minnesota	Level III ecoregions for assessing nonpoint source pollution and lake clarity, setting lake management goals, and for setting nutrient criteria	Heiskary and Wilson 1989; Heiskary and Lindon 2010; Olmanson et al. 2014
Nebraska	Level III and IV ecoregional guide to Nebraska birds and birding locations	Farrar 2004
Ohio	Level III ecoregions for stream biological criteria as part of state water-quality standards	Yoder and Rankin 1995,1998
Oregon	Level III ecoregions for state conservation strategy	Oregon DFW 2006
Tennessee	Level III and IV ecoregions for reference site selection and water-quality standards	Arnwine and Denton 2001a, 2001b
Federal agencies		
EPA	Modified Level II ecoregions for classifying and reporting stream, river, and lake assessments; multiple levels for ecological condition assessments	US EPA 2006, 2009, 2013; Stoddard 2004
USGS	Level II, III, and IV ecoregions to analyze trends, rates, causes, and consequences of land cover change in the conterminous United States	Auch et al. 2011, 2013; Drummond et al. 2012; Sleeter et al. 2012; Sleeter et al. 2013
USGS	Level III and IV ecoregions to assess factors controlling nitrogen and phosphorus distributions in Southeastern US streams	Hoos and McMahon 2009; Terziotti et al. 2010
USGS	Level III ecoregions to assess land cover change on albedo and radiative forcing	Barnes et al. 2013
USFS	Assessment of critical loads of nitrogen deposition in ecoregions of the conterminous United States	Pardo et al. 2011
Other		
NABCI (multiple agencies)	Modified North American ecoregions framework to facilitate a regional approach for the North American Bird Conservation Initiative (NABCI)	http://www.nabci-us.org/bcrs.htm
CEC and TNC	Level II North American ecoregions to assess and report on grassland priority conservation areas	CEC and TNC 2005
Native Seed Network	Level III ecoregion framework used for addressing native plant restoration and native plant seed industry marketing issues	http://www.nativeseednetwork.org/index
World Wildlife Fund	Modified Level III ecoregions as part of global ecoregion framework and conservation efforts	Olson et al. 2001

quality as pollution control practices are implemented, farming practices evolve, and watersheds undergo urban and industrial development (Iowa DNR 2001; Griffith et al. 1994b).

Ecoregions are particularly effective for integrating ecosystem management activities among resource management agencies and programs that use the same *pieces of the puzzle*, but aggregate them differently for different applications. The Tennessee Department of Environment and Conservation, for example, did not use the same groups of Level III and IV ecoregions for each of their applications; they used only those helpful for explaining patterns in each particular characteristic of water quality (Arnwine and Denton 2001a, 2001b). This example illustrates the need to understand the general purpose (versus special purpose) nature of ecoregions regarding assessment and management applications. As the relative importance of characteristics that in combination gives each ecoregion

its identity varies among regions so does that of the factors associated with different aspects of water quality and ecosystems. Spatial patterns of nitrogen concentrations in streams are not the same as those of phosphorus and neither of these are the same as patterns of alkalinity (Omernik 1977; Omernik and Powers 1983; Omernik et al. 1988). However, all are interrelated to many of the geographic phenomena (e.g., soils, vegetation, geology, geomorphology, and climate) subsumed in the identification of ecoregions, but each chemical characteristic is associated with land use, soils, and geologic factors differently. Hence, it is inappropriate to believe that all ecoregions at all levels are going to be ideal for any one particular aspect of aquatic or terrestrial ecosystems. Ecoregions are most helpful for aspects or indicators that reflect multiple factors of ecosystems, such as biological criteria, made up of a number of regionally calibrated metrics. Regarding water chemistry, Larsen et al. (1988) illustrated that while patterns in single chemical characteristics in Ohio streams were not associated well with all Level III ecoregions, when combinations of these characteristics were grouped in a principle components analysis with ionic strength variables on one axis and nutrient richness variables on the other, a strong ecoregion pattern could be seen.

One of the most comprehensive and effective uses of ecoregions on a national scale has been that of the USGS's land cover trends project that evaluates the rates, trends, causes, and consequences of land use and land cover change in the conterminous United States (e.g., Auch et al. 2011, 2013; Drummond et al. 2012; Napton et al. 2010; Sleeter et al. 2012, 2013). The regional framework has been used along with current and modeled future land cover to assess baseline and projected carbon storage in the United States (e.g., Zhu and Reed 2012) and to assess effects of albedo change and radiative forcing for the Eastern United States (Barnes et al. 2013). The USGS also found the framework helpful in the spatial analysis of nitrogen loads and factors controlling nitrogen delivery to streams (Hoos and McMahon 2009), in assessing phosphorus sources in streams (Terziotti et al. 2010), and in evaluation of the effects of urbanization on stream ecosystems in large metropolitan areas (Coles et al. 2012). The EPA has adapted Level II ecoregions to report the results of the National Rivers and Streams Assessment (U.S. EPA 2013b), the National Wadeable Stream Assessment (U.S. EPA 2006), and the National Lake Assessment (U.S. EPA 2009). Additionally, Level III and more detailed Level IV ecoregions have been used to explain patterns in nitrogen concentrations in the National Rivers and Streams Assessment (Omernik et al. in review). Another federal agency, the USFS, has used ecoregions to assess nitrogen deposition effects and empirical critical loads of nitrogen for the country (Pardo et al. 2011).

While many of the earlier applications of ecoregions related to aquatic resources, uses for other aspects of ecosystems including wildlife and forest management have grown. An example of a use at the continental scale is that of the North American Bird Conservation Initiative for structuring biological conservation research and planning (U.S. NABCI Committee 2000). At the national level, the Native Seed Network has used ecoregions for their research and guidance for restoration regarding native plant materials (http://www.nativeseednetwork.org/). State-level applications include the Nebraska Game and Parks Commission's and Georgia Department of Natural Resources' uses of Level III and IV ecoregions to classify areas of bird occurrence (Farrar 2004; Schneider et al. 2010). Level III and IV ecoregions were also used in Georgia as a framework for the natural communities of the state (Edwards et al. 2013). Many states use the ecoregions for their state wildlife action plans or conservation strategies, such as Oregon's use of Level III ecoregions (Oregon DFW 2006). Arkansas has adopted Level III and IV ecoregions for its multi-agency Comprehensive Wildlife Conservation Strategy (Anderson 2006) as has Alabama (Alabama DCNR 2005), Georgia (Georgia DNR 2005), Kentucky (Kentucky Department of Fish and Wildlife Resources 2013) and a few other states. The Arizona State Forestry Division used Level III ecoregions to structure a strategy to address forest-related conditions, trends, threats, and opportunities in their Arizona Forest Resource Assessment (Arizona State Forestry Division 2010).

Conclusions

A general ecoregion map of the conterminous U.S., which was first published 27 years ago (Omernik 1987), has evolved into a multi-authored hierarchical spatial framework. It has proven to be useful for many environmental applications. Driven by needs of environmental resource managers and scientists, the framework was refined and expanded to depict two coarser and one more detailed hierarchical levels. Interest by and support from the CEC, an international organization related to the North American Free Trade Agreement, resulted in collaborating with Canadian and Mexican experts in expansion of the framework into the remainder of North America. This expansion and improvement was attributable to the efforts and determination of a small team of geographers that worked with the principal author over these years, to the expertise of the more than 400 coauthors, collaborators, and reviewers of the ecoregions projects, to the ideas from the approximately 600 people total that participated in one meeting or another about advancing the ecoregion concept, and to the authors' confidence in the concept and utility of this ecoregion framework. And, as often occurs,

serendipitous events, lucky timing, and influential individuals were important factors in the development of an innovative tool. It was the right time to try to map such regions in terms of the evolution of the EPA as an institution and the science and regulation of water quality, particularly the development and implementation of the concept of regional stream reference sites. The timing was also fortuitous in the opening of the relatively short window of federal interagency cooperation that occurred when agencies including the USFS and the NRCS were revising their own natural resource frameworks and federal agencies were urged to work together for some common understanding of ecological regions.

In a paper on the search for synthesis in geography, Gober (2000) used a quote by Haggett (1975) to emphasize the need to move from, or at least complement, more reductive research with broader, more integrative and collaborative synthetic research. Haggett (1975) went even further and urged students to abandon comfortable reductive research and instead "focus on relationships between man and his environment, their spatial consequences, and the resulting regional structures that have emerged on the earth's surface." This is essentially what the synoptically developed ecoregions are about. Gober (2000) also noted some barriers to synthesis, similar to some of the difficulties we have found in getting people to understand the nature of ecoregions and how they are defined. Gober expressed her frustration that "ecologists, geologists, and engineers mean different things when they use words like population, disturbance, network, system, and hierarchy." Hence, the dilemma expressed by Julian Campbell that there is no perfect ecoregion map because there are too many viewpoints, biases, and applications to allow its definition (Julian Campbell 2000, personal communication). We recognize this lack of agreement, the general discomfort with mapping something as spatially and temporally complex as ecoregions, and the tendency for many to be more comfortable with single purpose frameworks. However, we are encouraged by the comments of the researchers and resource managers we have encountered, and by the wide variety of applications in which the framework has proven useful. Its strengths include its consistency in its compilation, a scale and hierarchy that has utility, its input from a large number of individuals and disciplines, and regions and boundaries that users on the ground readily recognize.

We have attempted here to explain some of the mapping process that has led to the present hierarchical framework of ecological regions, but important work remains to improve the framework, clarify its strengths and limitations regarding the increasing number of applications, and improve our collective understanding of regional ecological patterns of the nation. Additional research and documentation of the apparent regional associations of geographic phenomena within Level III and IV ecoregions, including information learned in the mapping process, would be useful for a wide variety of disciplines. Future research is needed especially on analyzing change in the characteristics of ecoregions and in ecoregion boundaries. The USGS in its land use/land cover work has found that because the capacities and tolerances of ecoregions are different from one region to another, regardless of the hierarchical level, they are changing differently for different human and nonhuman-related reasons, and that this has important implications for environmental management decisions, including those regarding climate change (Gallant et al. 2004; Sleeter et al. 2012). Along with more detailed historical narratives of ecological change, research is needed on how modifications by anthropogenic activities, such as the increasing extent of urbanization and industrialization or expansion of agriculture, or changing climatic conditions, might affect the definition of ecoregions.

Acknowledgments The authors would like to thank the numerous people who helped map, author, review, fund, promote, or otherwise provide support in the development of the ecoregion framework discussed in this paper. While there are many individuals who should be acknowledged, special thanks are given (alphabetically) to the other members of our geography team who did large portions of the research, writing, and mapping of the nation, especially Sandy Bryce, Shannen Chapman, Alisa Gallant, and Alan Woods; to those who provided other technical, research, or organizational support including Sandy Azevedo, Doug Brown, Sharon Clarke, Jeff Comstock, Jerry Freeouf, Andy Herstrom, Hoke Howard, Colleen Burch Johnson, Duane Lammers, Chad McGrath, Henry McNab, Brian Moran, David Pater, Sue Pierson, Ben Sleeter, Dave Smith, Thor Thorson, Marc Weber, Denis White, and Ed Wiken; and to those who helped with the institutional support and fundamental design including Mike Beiser, Phil Crocker, Jack Gakstatter, Jim Harrison, Bob Hughes, Phil Larsen, Rick Linthurst, Tom Loveland, Jerry McMahon, Tony Olsen, Steve Paulsen, Tony Selle, Safa Shirazi, John Stoddard, Tom Wilton, and Chris Yoder.

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