# CHAPTER 4

# Isotope Landscapes for Terrestrial Migration Research

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## Contents

*Tracking Animal Migration with Stable Isotopes*
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## I. INTRODUCTION

Isotope tracking of migratory terrestrial animals (*e.g.*, birds, bats, and insects) relies on the assimilation and fixation of intrinsic isotopic markers from the environment into animal body tissue. The power of the isotopic markers relates to the extent and pattern of spatial isotope ratio variations in the environmental substrates from which they are assimilated (primarily food, water, and air). This chapter introduces these patterns of variation for most of the commonly applied or applicable stable isotope systems, and describes methods by which the spatial landscapes of environmental isotopic variation ("isoscapes") are modeled and predicted at scales relative to the study of migratory behavior and ecology. Examples of isoscapes for some isotopic systems are presented along with discussion of challenges and cautionary notes related to the creation and interpretation of isoscapes. A discussion of opportunities and future directions in isoscape modeling is offered. The goal of this chapter is to familiarize the researcher with isoscape data products and the range of current and potential products for use in migration applications. Also described are the principles and methodology underlying the development of these products and relevant to their informed use.

Maps of some isotopic landscapes have been available since the early 1980s, when workers affiliated with the International Atomic Energy Agency (IAEA) and World Meteorological Organization's Global Network for Isotopes in Precipitation (GNIP) compiled and contoured mean annual precipitation isotope ratio data to produce a map with near-global coverage (Yurtsever and Gat 1981). The GNIP data set has remained a prime example of a spatial isotope monitoring network, providing a data set that has motivated the development of improved isoscapes for H and O in water (Birks *et al.* 2002, Bowen and Wilkinson 2002, Bowen and Revenaugh 2003, Meehan *et al.* 2004, Bowen *et al.* 2005, Bowen *et al.* 2007) and, more recently, for plants (West *et al.* in review).

Isoscapes of ecosystem-scale carbon isotope ratios were found to be relevant to the study of the global carbon cycle using $\delta^{13}C$ and have been in development since the early 1990s (Lloyd and Farquhar 1994, Still *et al.* 2003, Suits *et al.* 2005). The development of isoscapes for other isotopic systems is very recent, and preliminary attempts to represent plant and soil nitrogen isoscapes (Amundson *et al.* 2003) and Sr isoscapes (Beard and Johnson 2000) have appeared in the literature in the last few years.

Research on the spatial patterning of isotopes in the environment and their modeling and depiction is an active field, and although some data products are well documented and publicly available through websites such as http://www.waterisotopes.org, the scope of these products is currently limited. Given that much of the data, theory, and software enabling isoscapes modeling are freely available, a secondary goal of this chapter is to introduce many of the fundamental considerations underlying isoscapes modeling in hope of encouraging additional researchers to participate in the future research and development of isoscapes relevant to migration research, in particular to tackle such questions as connectivity, movement across landscapes, and intra- and interspecific habitat use at various spatiotemporal resolutions.

## II. PROCESS

Mapping isotopic variations across space is accomplished through the identification, simplification, and modeling of the processes that lead to isotopic variations at the landscape level. Although a wide range of physical and chemical processes can produce isotopic discrimination and contribute to observed isotope distributions, a relatively small subset of processes dominates landscape-level variability. We begin by highlighting and reviewing these processes as they relate to isoscape modeling for terrestrial migration studies.

## A. Rayleigh Distillation and Precipitation $\delta^2$H and $\delta^{18}$O

Global spatial variability in the isotopic composition of meteoric precipitation (rainfall) was first reported by Dansgaard (1954, see also Craig 1961, Dansgaard 1964), making it one of the longest-studied examples of landscape-level isotopic variation. The profound variation in $\delta^2$H and $\delta^{18}$O values measured for precipitation samples collected worldwide (Rozanski *et al.* 1993) can largely be attributed to a single phenomenon: the progressive drying of air masses as they lose moisture in the form of precipitation. The phase change reaction that leads to the formation of water droplets (or ice crystals) in clouds proceeds with an equilibrium isotope effect $\alpha_e$ through which water molecules containing heavy isotopic species are preferentially incorporated in the liquid or solid phase during condensation (note that $\alpha_e$ differs for condensation to liquid vs solid phase and for $^2$H- and $^{18}$O-bearing water molecules). Having grown to a size at which they fall from the convecting cloud mass, rain droplets or snow crystals are effectively removed from the cloud system, taking with them a disproportionate concentration of the "heavy" isotopic species and leaving the cloud vapor incrementally depleted in $^2$H and $^{18}$O. As this process proceeds, the $\delta^2$H and $\delta^{18}$O values of the cloud vapor become progressively lower according to the Rayleigh equation (given in terms of ratios):

$$R = R_0 f^{(\alpha-1)} \tag{4.1}$$

where $R$ is the isotope ratio of cloud vapor at any point in time, $R_0$ is the initial isotope ratio of the air mass, and $f$ is the fraction of vapor remaining. For the residual vapor produced through the condensation process, values of $\alpha$ are less than 1, giving a progressive decrease in vapor isotope ratios (and those of newly formed precipitation) as an air mass dries.

## B. Hydrological Mixing, Evaporation, and Surface Water $\delta^2$H and $\delta^{18}$O

The primary postprecipitation processes affecting the stable isotopic composition of continental waters are hydrological mixing of waters having different isotopic compositions and reevaporation from the land surface. Large data sets of H and O isotope ratios of river and tap water clearly show the impact of both processes on spatial variation in environmental water isotopic compositions (Kendall and Coplen 2001, Bowen *et al.* 2007). Mixing represents a linear process, weighed according to the volumetric concentration of the different sources. Mixing is a particularly important process where waters are present that have very different isotopic compositions because they fell at different times or places (*e.g.*, mountain snowmelt and summertime basinal rain in mountainous regions) or have different postprecipitation histories (*e.g.*, thermal spring water and surface water).

Reevaporation of water can occur at many points in the postprecipitation history of all continental waters, including from leaf surfaces that intercept falling rain, soils, rivers, lakes, or reservoirs. Isotope fractionation during evaporation does not follow a simple equilibrium model but involves a dynamic balance of the phase change reaction and bidirectional diffusive transport between a boundary layer adjacent to the liquid surface and the free atmosphere. These processes were synthesized as the "Craig–Gordon model" (Craig and Gordon 1965):

$$\frac{d\delta}{d\ln f} = \frac{h(\delta - \delta_a) - (\delta + 1)(\Delta\varepsilon + \varepsilon/\alpha)}{1 - h + \Delta\varepsilon} \varepsilon_t = \varepsilon_e + \Delta\varepsilon_k, \tag{4.2}$$

where $\delta$ and $\delta_a$ are the isotopic compositions of the evaporating water body and atmosphere, $f$ is the remaining fraction of liquid, $h$ is atmospheric humidity, and $\varepsilon$, $\alpha$, and $\Delta\varepsilon$ are the isotope effect and fractionation factor for equilibrium evaporation, and the kinetic isotope effect of evaporation, respectively. Under low-humidity conditions, evaporation can be approximated as distillation process following Eq. (4.1). The net isotope effect of evaporation is to increase the $\delta^2$H and $\delta^{18}$O values of residual surface water, with the magnitude of change scaling with the extent of evaporation and affected by $h$ and other parameters that determine the evaporative fractionation.

## C. Plant Water and Organic H and O Isotopes

The rainfall isotopic patterns discussed in Section II.B are intimately connected to the base of all terrestrial food webs through the linkage of water and primary productivity (plants). To a first approximation, the isotopic composition of the water in plants may be simplified to two pools: unfractionated water that essentially matches the plant source water isotopic composition (*e.g.*, xylem water derived from soil water) and $^2$H- and $^{18}$O-enriched leaf water. Leaf water isotope ratios increase in response to evaporation in a manner analogous to open water bodies, with liquid to gas phase changes occurring inside the leaf, diffusion of vapor through stomatal openings and the leaf boundary layer, and isotopic exchange of leaf water with atmospheric vapor. These isotope effects have been described in several models of leaf water enrichment, derived principally from the Craig–Gordon model. The general equation for steady state leaf water isotope ratios has been written as:

$$R_e = \alpha\left[\alpha_k R_S\left(\frac{e_i - e_s}{e_i}\right) + \alpha_{kb} R_S\left(\frac{e_s - e_a}{e_i}\right) + R_A\left(\frac{e_a}{e_i}\right)\right] \tag{4.3}$$

where $R_e$ is the isotope ratio of evaporated leaf water, $R_S$ is the isotope ratio of the source water, $R_A$ is the isotope ratio of the atmospheric water vapor, $e_i$ is internal leaf vapor pressure, $e_s$ is the leaf surface vapor pressure, and $e_a$ is atmospheric vapor pressure (Flanagan *et al.* 1991). Other models incorporate additional complexities found to be important, including nonsteady state dynamics (Dongmann *et al.* 1974, Farquhar and Cernusak 2005) and within-leaf heterogeneity, including back-diffusion of heavy isotopes in liquid leaf water (Yakir *et al.* 1994, Helliker and Ehleringer 2000, Péclet effect; Farquhar and Cernusak 2005).

Leaf water isotopic composition is important both because leaf water is a potential source of animal body water (*e.g.*, Murphy *et al.* 2007) and because the isotopic composition of plant organic molecules is dependent on the isotopic composition of the water at sites of photosynthesis in leaves, as well as the isotopic effects of photosynthesis itself and other biochemical transformations during plant metabolism (Roden *et al.* 2000). These isotope fractionations can be relatively large. For example, observed fractionation factors for the formation of cellulose are $\varepsilon = 27$‰ for oxygen isotopes and $\varepsilon = 158$‰ for hydrogen isotopes (Sternberg and Deniro 1983, Yakir *et al.* 1990, Luo and Sternberg 1992).

## D. Gas Exchange, Photosynthetic Pathway, and Plant C Isotopes

The carbon isotope ratios of plant tissues are dependent on the $\delta^{13}$C of atmospheric $CO_2$ and the isotope fractionation events that occur during carbon fixation, including diffusion, dissolution, and hydration of $CO_2$, and the fixation reactions themselves (Park and Epstein 1960, Osmond *et al.* 1973, Farquhar *et al.* 1989, O'Leary *et al.* 1992, Von Caemmerer 1992, Ehleringer and Monson 1993). There are three primary pathways of carbon fixation in plants: $C_3$, $C_4$, and CAM, names that refer to the number of carbon atoms in the first stable product of photosynthesis ($C_3$ and $C_4$) or the nocturnal buildup of malic acid (CAM). The $C_3$ pathway utilizes ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) as a catalyst to form a three-carbon molecule from atmospheric $CO_2$ during the day. The $C_4$ pathway is primarily found in grasses and utilizes phosphoenolpyruvate (PEP) carboxylase as a catalyst to fix $HCO_3^-$ (atmospheric $CO_2$ hydrated in a reaction catalyzed by carbonic anhydrase) initially to a four-carbon molecule that is then the source of $CO_2$ for $C_3$ photosynthesis. In $C_4$ plants, the $C_3$ photosynthesis phase is generally spatially isolated from the atmosphere and receives high concentrations of $CO_2$ from the PEP carboxylase system. CAM plants also utilize PEP carboxylase to catalyze the first step, but rather than isolate Rubisco spatially as occurs in $C_4$ plants, these plants do the initial step of fixing $CO_2$ at night when the vapor pressure deficit is lower. Rubisco strongly discriminates against $^{13}CO_2$ (~30‰ O'Leary 1981) giving $C_3$ plants strongly $^{13}$C-depleted carbon isotope ratios. PEP carboxylase, on the other hand, shows much lower discrimination (~2‰) that results in $C_4$ plants having higher $\delta^{13}$C values (CAM plants show a wide range of values; Ehleringer *et al.* 1986).

The differences in isotopic discrimination between these two enzymes are large enough that $C_3$ and $C_4$ plants have nearly completely nonoverlapping carbon isotope distributions (Ehleringer *et al.* 1986). This was observed very early in the study of stable isotope ratios in plants (Wickman 1952, Craig 1953), and has been utilized extensively to understand plant–animal interactions, both in modern environments and in paleoenvironments (*e.g.*, Van Der Merwe *et al.* 1988, Cerling *et al.* 2003).

Stomatal resistance has an important effect on the carbon isotope ratios of $C_3$ plants. The number and aperture of stomates control the $CO_2$ diffusion resistance between the atmosphere and the substomatal cavities, and thus determines the relative openness of the isotopic system with respect to the source $CO_2$. As stomates close, the supply of $CO_2$ to the substomatal cavity, as well as its diffusion back out of the leaf, slows. This slowing of $CO_2$ exchange with the atmosphere results in a relative $^{13}$C enrichment of the products of photosynthesis because of a progressive $^{13}$C enrichment of the internal leaf $CO_2$ pool and a proportional increase in the flux of $^{13}CO_2$ into the reactions of photosynthesis. Because of this effect of stomatal aperture, climate exerts a dominant influence on the carbon isotopic signature of $C_3$ plant tissues. With greater water limitation, stomates tend to close, increasing the $\delta^{13}$C of the resulting sugars and ultimately other organic materials in plants (Hemming *et al.* 2005).

## E. Nitrogen Isotopes in Soils and Plants

Plant $\delta^{15}$N is determined by the isotopic composition of the plant N source and the isotope fractionations associated with plant N uptake and metabolism. Because there are multiple, competing reactions in soils, many of which have strong isotopic effects, a general theory describing soil $\delta^{15}$N has not yet emerged (Evans 2001, Robinson 2001). Primarily because of this, plant nitrogen isotopic composition has been generally interpreted as an integrator of the effects of important processes that can inform questions related to changes in N cycling and sources, but that needs to be interpreted cautiously and in primarily site-specific ways (Evans 2001, Robinson 2001). Large-scale comparisons have shown correlations between both the $\delta^{15}$N of plants and soils and climate variables such as mean annual temperature and precipitation (Austin and Sala 1999, Handley *et al.* 1999, Amundson *et al.* 2003, Ometto *et al.* 2006). Although much of the global observed variability remains unexplained by these simple models, they do suggest dominant controls on soil–plant $\delta^{15}$N based on preferential losses of $^{15}$N from systems (cf. Houlton *et al.* 2006). Clearly, inputs are an important control on plant and soil $\delta^{15}$N also because N fixation inputs are near 0‰, but can vary from −3‰ to 1‰ (West *et al.* 2005) and nitrogen deposition can vary considerably, depending on the nitrogen source (Pardo *et al.* 2006, Widory 2007). More recent work suggests the tantalizing possibility that remotely sensed reflectance data might yield information on vegetation $\delta^{15}$N (Wang *et al.* 2007).

## F. Ecosystem Sr Isotopes

Isotopic variation in Sr, unlike that in the other light isotope systems discussed here, is driven by the continuous production of one of the common isotopes, $^{87}$Sr, which forms during the $\beta^-$ decay of $^{87}$Rb. Both the radiogenic isotope $^{87}$Sr and the more common, nonradiogenic $^{86}$Sr are stable, and differences in the relative abundance of these isotopes due to the level of production of the radiogenic isotope are tracers of Sr source. Because the half-life of $^{87}$Rb is quite long (~48.8 billion years), production of $^{87}$Sr occurs over geological timescales and much of the potential Sr isotope variability in and among ecosystems is related to the type and history of the rocks from which their Sr is derived. Variation in the $^{87}$Sr/$^{86}$Sr of rocks occurs for a number of different reasons, including variation in the initial Sr isotope ratio of igneous rocks and carbonate rocks at the time they solidify from magma, variation in the $^{87}$Rb content of different rocks, and variation in the age of rocks (Faure and Powell 1972).

When considering variation in ecosystem Sr isotope ratios that might be sampled by a migrating animal, however, isotopic variability of rock Sr only represents the base layer of variability at the landscape level [*e.g.*, see review by Capo *et al.* (1998)]. Rock Sr is released to ecosystems by weathering, and in areas where multiple rock sources are available, Sr isotope ratios within ecosystems can be heavily biased toward those of Sr sourced from individual rock types. In many cases, ecosystem $^{87}$Sr/$^{86}$Sr is largely determined by those of carbonate rocks that weather rapidly and have total Sr concentrations approximately two to six times higher than most other rocks (Faure and Powell 1972). Sources of Sr entering groundwater, surface water, and soils can often differ, particularly in areas where windblown dust contributes a significant fraction of Sr to soils (*e.g.*, Quade *et al.* 1995, Kennedy *et al.* 1998) or where bedrock geology is particularly heterogeneous, meaning that multiple, isotopic distinct pools of Sr may be available to plants and animals living in proximity. Nonetheless, spatial variability in $^{87}$Sr/$^{86}$Sr, primarily because of major variation in rock type distributions over large spatial scales, has been shown to propagate into ecosystems and represent a useful tracer for migratory ecology and paleoecology (*e.g.*, Chamberlain *et al.* 1997, Hoppe *et al.* 1999).

# III. PATTERN

The processes discussed in the previous sections produce spatial isotope variations in the environment, but in order to understand the existence of systematic, predictable, isotopic variability that is useful for terrestrial migration research, we must consider the organization of these processes with respect to space. Indeed, the fact that many isotopically discriminating processes are spatially patterned underlies the isoscapes concept and the correlative application of stable isotope tracking in migration research. The creation of isoscapes for migration research requires that these patterns be mapped in space, usually through the mathematical transformation of maps depicting correlates or environmental drivers of isotopic variation. We will first review the origin of these patterns, considering how they relate to geological, physiographic, climatological, and biological (collectively, "environmental") drivers, and then introduce a two-endmember classification system for spatial patterning of isotopic variation.

## A. Spatial Organization and Isotope Patterning

Stable isotope variations in the environment reflect the spatial patterning of environmental factors in three primary ways. First, geographic position can determine the elemental sources available for incorporation in biological substrates, and thus impact the isotopic composition of ecologically relevant materials. Second, where isotopes are fractionated by environmental processes, the magnitude of fractionation at a given site will respond to local environmental conditions. Third, for systems in which large-scale geographic transport is important, the spatial organization of transport processes (*e.g.*, atmospheric circulation, runoff, groundwater flow) will determine both the isotopic source and the integrated history of fractionating processes, affecting material in the local environment. Each of these modes relating isotopic variation to spatially varying environmental parameters can be illustrated through examples from the systems introduced earlier.

Spatial variation in the isotopic composition of elemental sources is important in all systems where these sources exhibit landscape-level isotopic heterogeneity, and in many cases may be the primary determinant of the isotopic composition of biological systems. Strontium isotopes, which are not measurably fractionated by biological systems, provide an example system in which spatial variation in elemental sources controls the isotopic composition of plants and animals. Work by Kennedy *et al.* (1998) on the well-characterized soil chronosequences of the Hawaiian islands nicely illustrates such a relationship. In this case, soils that are initially charged with Sr from the bedrock basalt exist in a dynamic balance where Sr lost through weathering and leaching from soils is replenished by Sr inputs from oceanic aerosols. Because the basalt and marine Sr sources have very different $^{87}Sr/^{86}Sr$ values, it is primarily land surface age, in turn determined by the age of the bedrock basalt flows, that is the primary determinant of Sr isotope ratios in soils and plants. The ages of basalt flows, both on the Big Island of Hawaii (Figure 4.1A) and throughout the island chain, are spatially patterned, creating a strong spatial patterning of Sr isotope ratios in Hawaiian island food webs.

In isotopic systems in which appreciable isotopic fractionation occurs in the environment and biological systems, spatial variation in the local environmental conditions under which isotope-fractionating processes occur can have a large impact on the isotopic composition of plants and animals. The photosynthetic assimilation of carbon by plants, for example, is a highly fractionating process that uses carbon from a relatively isotopically homogeneous environmental substrate, atmospheric $CO_2$. As such, there is relatively little potential for spatial isotopic variation in elemental sources to drive variation in plant $\delta^{13}C$ values (with exceptions such as near urban centers; Pataki *et al.* 2003), but great potential for variation in the *magnitude* of photosynthetic fractionation to produce spatial $\delta^{13}C$ variation. For $C_3$ ecosystems, photosynthetic discrimination is largely controlled by environmental parameters such as soil water availability, temperature, and atmospheric moisture content that influence the gas exchange physiology of leaves. As a result, strong relationships often exist between climate variables such as temperature or precipitation and plant or ecosystem $\delta^{13}C$, leading to spatial patterning of carbon isotope ratios that mimics variations in climate. This is nicely illustrated by measurements of the $\delta^{13}C$ of ecosystem respiration along a sampling transect in western Oregon (Figure 4.2; Bowling *et al.* 2002) that demonstrates a strong relationship between ecosystem carbon

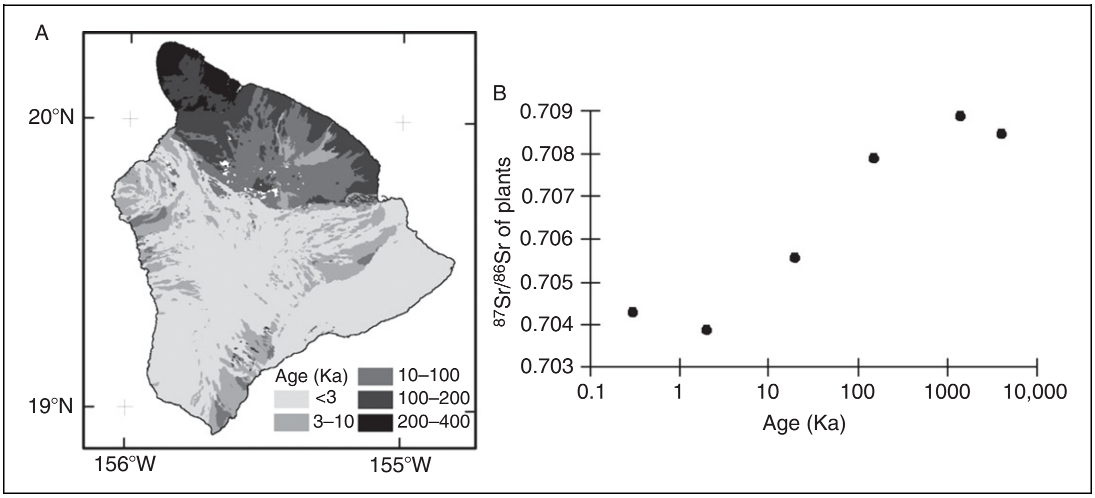

**FIGURE 4.1** Spatial patterning of an environmental property underlying variation in ecosystem Sr isotope ratios on the Big Island of Hawaii. (A) The spatial distribution of approximate landscape surface ages (after Trusdell *et al.* 2006) on the Big Island of Hawaii. (B) A strong relationship exists between surface age and plant $^{87}Sr/^{86}Sr$, reflecting the decreased availability of basalt-derived Sr and increased accumulation of Sr from sea-salt aerosols with greater surface age (Kennedy *et al.* 1998).

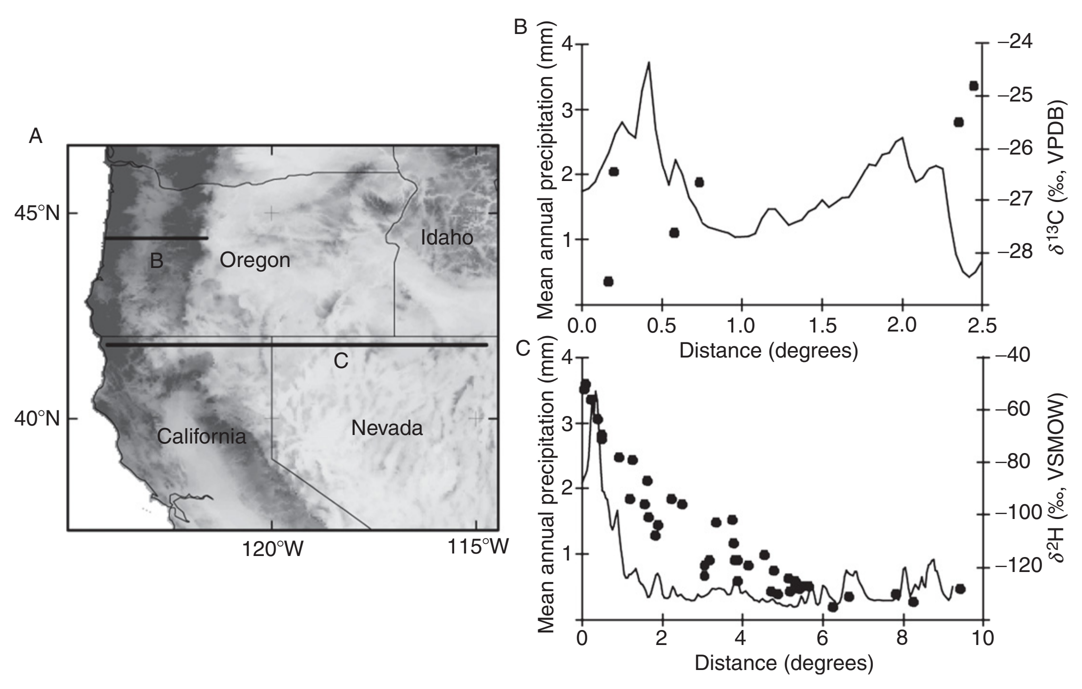

**FIGURE 4.2** Landscape-level stable isotope variation related to spatial patterning of climatic gradients. (A) Strong gradients in mean annual precipitation amount (Daly *et al.* 1994) characterize two western US isotope sampling transects (bold lines). (B) Carbon isotope ratios of ecosystem respiration (dots, estimated from Keeling plots; Bowling *et al.* 2002) show a strong relationship to position along the Oregon transect, and are broadly, negatively correlated with precipitation amount (line). This reflects the strong relationship between local fractionation due to plant gas exchange processes and climatology along the spatial climate gradient. (C) Hydrogen isotope ratios of meteoric water samples (groundwater, springs, and streams; Ingraham and Taylor 1991) varying continuously along a transect in northern California and Nevada are positively correlated with changes in precipitation amount along the coast to interior gradient. The gradients in the water isotopic composition and precipitation amount can each be related to variation in the processes governing air mass water balance and transport along the dominant westerly atmospheric circulation trajectory for this region.

isotope ratios and precipitation amount along a strong, coast-to-continent gradient in precipitation amount.

The third, and most complex, type of relationship linking spatial isotopic variation to spatial variation in environmental factors is found in cases where transport history is a primary determinant of isotopic composition. We have seen, for example, the isotopic composition of meteoric precipitation is dependant, among other factors, on the condensation history of the air mass from which the precipitation forms. As a result, $\delta^2$H and $\delta^{18}$O values of precipitation can not be predicted *a priori* without consideration of the trajectory taken by the atmospheric moisture, reaching the site at which the precipitation condenses. Spatial organization clearly exists at many levels within the climate system, however, including atmospheric circulation patterns and the temperature gradients that lead to condensation from air masses, leading to spatial patterning in transport and condensation history of precipitating air masses. Waters sampled along a gradient in mean annual precipitation amount from the northern California coast to eastern Nevada (Figure 4.2; Ingraham and Taylor 1991), for example, illustrate a strong, spatially determined relationship between precipitation amount and isotopic composition, which reflects the progressive drying of air masses leaving the northern Pacific Ocean and traversing western North America.

## B. Two Classes of Isotopic Patterns

Spatial patterning of isotopic variation in many systems closely mimics that of the underlying environmental determinants. This isotopic patterning can take on a range of forms depending on the spatial distribution of variation in environmental parameters, and its form has important implications for the types of migration research applications to which each isotope system is suited. In this context, we distinguish two endmember classes: spatially continuous and spatially discrete patterns. Depending on the environmental determinants of spatial variation in a given isotope system and the spatial scale in question, isoscapes can depict isotopic variation that is spatially continuous, discrete, or intermediate to these endmember classes.

Spatially continuous isoscapes are characterized by smooth variation in isotope ratios across space, giving continuous isotopic gradients along map transects. These isoscapes occur in cases where the underlying environmental determinants vary continuously in space and the process through which they impact landscape-level isotope ratios is a continuous function. Continuous isoscapes are common but not ubiquitous where climatological factors drive isotope ratio variation: for example, the continuous (though not unidirectional) change in precipitation amount that is related to ecosystem $\delta^{13}C$ values in western Oregon or the progressive rainout of moisture during westerly circulation, driving precipitation $\delta^{2}H$ variation across northern California and Nevada (Figure 4.2).

Spatially discrete isoscapes represent the contrasting pattern of spatial variation in which isotope ratios of environmental substrates are relatively invariant over some areas but change abruptly and discretely across the boundaries between invariant zones. Such patterns of "patchy" spatial isotopic variation can occur where environmental drivers vary discretely across space or where continuously varying environmental factors influence isotopic variability according to discrete functions. Isotopic variation of Sr in Hawaiian island ecosystems (Figure 4.1) represents an excellent example of the first scenario, where the aerial extent of individual lava flows define land surfaces of common age, presumably characterized by similar ecosystem Sr isotope ratios, and the discrete boundaries of these flows segment the isotopic landscape. The second scenario can be illustrated by the case of natural, climate-induced variation in the distribution of $C_3$ and $C_4$ plants. Although driven by continuously varying climate parameters, the impact of climate on $C_4$ distribution (and thus ecosystem $\delta^{13}C$ values) is described by a threshold function (Ehleringer *et al.* 1997, Collatz *et al.* 1998), and in many cases the distribution of these plant types can be considered to be discrete, particularly over large spatial scales (Still *et al.* 2003). The issue of scale is highly relevant to the concept of discrete isoscapes, as both transport processes and statistical variance in populations tend to smooth the boundaries of discrete isoscapes, particularly at small spatial scales.

The recognition and distinction of isoscape pattern classes is critical for terrestrial migration ecology applications in that they largely determine the types of ecological questions to which different isotopic systems are applicable. Continuous isoscapes offer important, recognized opportunities for research in migratory connectivity, particularly at large spatial scales. Because isotope ratio variation within continuous isoscapes is largest along directional, environmental gradients, these isoscapes are most amenable to addressing questions dealing with the position of individuals along geographic gradients. The continuous isotope ratio variation across these isoscapes can confound attempts to apply them to questions of explicit assignment of individuals to discrete locations, although statistical assignment techniques have been successfully applied to questions that can be posed as assignment to regions (Chapter 5; Wunder *et al.* 2005). Discrete isoscapes are well suited in some cases to address assignment questions where the questions and constraints can be well defined and overlap with isotopically defined spatial domains. However, isotope systems that are characterized by discrete spatial patterning cannot be applied to assignment at spatial scales below that of the patches comprising the isoscape, and depending on the environmental forcers involved potential exists for nonunique assignments within the domain of study.

Published applications of isotopes to terrestrial migration research have capitalized on both classes of patterns. With the advent of hydrogen isotope ratios as a tool for wildlife forensics (Chamberlain *et al.* 1997, Hobson and Wassenaar 1997), much emphasis has been focused on the application of continuous isoscapes of $\delta^2$H in water to problems of migratory connectivity. However, several examples focusing on reconstructing the migration of modern or ancient animals and humans continue to exploit discrete spatial variability of isotope ratios, in particular those of Sr (Chamberlain *et al.* 1997, Hoppe *et al.* 1999). The relative strengths and weaknesses of each class of isoscape should be considered in future application, and in particular, we suggest that important opportunities exist for coupling isotope systems with continuous and discrete isoscapes characterized by variation at different spatial scales.

## IV. MAPPING ISOSCAPES

Isoscape maps are created through a multistep process that is often iterative. Information on isotope fractionating processes and patterns, represented as models, is combined with geospatial data to produce site-specific isotope ratio predictions over a spatiotemporal domain of interest. Major steps in the process include model selection, model calibration, data acquisition, calculation, optimization of model residuals, and estimation of error.

### A. Model Selection and Calibration

For many isotope systems, multiple models are available, or could be envisioned, to describe the fractionating processes determining spatial isotopic variability within the system. These may range in complexity and precision from purely theoretical first-principals equations to highly derived empirically calibrated functions. In many cases, trade-offs exist between the accuracy of a model and its ability to be generalized or applied over large spatial scales. Appropriate model selection is critical to obtaining an accurate and well-constrained isoscape for the system and spatiotemporal domain under consideration, and these factors together with the availability of data and intended uses of the product should guide the choice of model.

The least-specific classes of models that can be applied to any isotopic system are geostatistical interpolation models. These models describe the variation in isotope ratios in terms of location alone. Estimates are calculated as a function of observed values at nearby locations, meaning that the only data required are observations of the isotopic ratio at points within the spatial domain of interest. A range of interpolation models of varying complexity are available, and some of the simpler examples such as triangulation, nearest neighbor, and inverse distance techniques are widely applied by non-specialists. The only statistically "correct" method for spatial interpolation is known as kriging that is the name given to a class of procedures in which the weights assigned to nearby data during the interpolation process are determined by a model of the covariance structure of the observational data (Isaaks and Srivastava 1990). Interpolation models offer a convenient way of visualizing and extending observations from a well-developed sampling network across space, but the degree of detail in the resulting isoscape is entirely limited by that represented in the measured or observational data set. As a result, the use of interpolation models in isolation is best restricted to cases where the observational documentation of spatial isotopic variation is extensive. However, as we will see in the following sections, interpolation models can be used to improve isoscape accuracy when used in combination with other types of models.

More specialized models for spatially varying isotopic systems can be constructed using derived parameters as proxies for the environmental factors underlying the isotopic variation. These models are particularly useful in cases where the complexity or data requirements of first-principles or process-based models are prohibitive, but where a simpler or more readily obtained suite of surrogate parameters can be substituted in their place. Derived models have been used to create global isoscapes of precipitation isotope ratios by simplifying the extremely complex suite of environmental factors underlying spatial isotopic variation in precipitation to a derived model of the form:

$$\delta = a(L^2) + b(L) + c(A) + d, \tag{4.4}$$

where $\delta$ is the isotopic composition of precipitation, $L$ is latitude, $A$ is altitude, and $a$, $b$, $c$, and $d$ are empirically fitted parameters (Bowen and Wilkinson 2002). As this example shows, the parameters used in derived models may be only indirectly related to the physical processes driving isotopic variation, but may be useful surrogates because of correlation with the first-order parameters. In most cases, parameter values will need to be calibrated relative to observational data, but if the model is stable and the parameters are skillfully chosen, some derived models will be capable of extrapolation to combinations of parameter values not represented in the observational data set.

A third class of models includes first-principles and process-based parameterizations. Because of the complexity of the processes underlying isotopic variability, there are few cases where models can be fully developed based on first principles alone. Where such models could be developed, it is likely that they would necessarily oversimplify the systems of interest, severely limiting their applicability. For example, a first-principles model of the radiogenic production of $^{87}$Sr could be applied using data on rock ages and Rb contents to produce a bedrock $^{87/86}$Sr map, but this isoscape would likely have limited relevance to $^{87/86}$Sr of most terrestrial ecosystems because of reasons discussed above. In contrast, process-based models strive to faithfully represent the physical and chemical processes underlying isotopic variation but adopt parameterizations that may group or simplify the details of these processes. For example, commonly used models of photosynthetic $^{13}$C fractionation by $C_3$ plants explicitly represent the biophysics of $CO_2$ gas exchange by leaves but incorporate species-specific or biome-specific parameters to describe the biological regulation of gas exchange by the stomata (Ball *et al.* 1987, Lloyd and Farquhar 1994). These model parameters must again be calibrated against field data, but given the more fundamental nature of these variables, this work can often be done through laboratory studies or experiments and extended to the spatiotemporal domain.

## B. Geospatial Data

A mind boggling amount of geospatial data currently available to support scientific research are found in the form of digital data archives, reanalysis and data synthesis projects, GIS database and decision support tools, and real-time Earth-observing satellite data. Many types of geospatial data are relevant to isoscapes modeling, including physiographic information (*e.g.*, position data such as latitude and longitude, elevation, land surface slope), climate data (*e.g.*, temperature, precipitation amount, atmospheric humidity), geological data (*e.g.*, bedrock geological maps, soil types), hydrological data (*e.g.*, stream routing, aquifer distribution and depth), biological data (*e.g.*, species or biome distributions, leaf area index, the normalized difference vegetation index), and socioeconomic and demographic data (*e.g.*, distribution of crop production, population density, land use).

Major data distributors include the World Data Center System, the National Aeronautics and Space Administration, the National Center for Atmospheric Research, Oak Ridge National Laboratory Distributed Active Archive Center, the National Oceanic & Atmospheric Administration, the US Geological Survey, the Climatic Research Unit, the European Centre for Medium-Range Weather Forecasts, and synthesis projects such as The International Satellite Land-Surface Climatology Project. Depending on the data type and provider, differing levels of spatial and temporal coverage may be available: many data sets are available for individual states or countries, and the temporal sampling interval of satellite-gathered data may be widely different from ground-based observational products. These issues must be taken into account and reconciled, for example, through creating mosaics of data from multiple sources or averaging data over a common time window, before the data can be used in isoscapes models.

Because the end goal of isocapes modeling is to produce continuous surfaces of isotopic variation in space, the data input to these models must be amenable to representation in raster format. A raster is a representation of data in two or more dimensions (*e.g.*, latitude and longitude for many geospatial rasters) as a grid of regularly spaced cells, each containing a single value. Rasters are a limited data format, in that each grid can only contain values for a single parameter, but they are useful for isoscapes modeling in that they are continuous (*i.e.*, they provide values or “no data” indicators for the entire spatial extent of the raster) and many rasters can be formatted uniformly to allow them to be combined and analyzed together. Many geospatial data are distributed in raster format, and others can be easily converted (*e.g.*, a polygon that represents the aerial extent of a biome can be converted to a raster grid of 1s and 0s, representing the presence or absence of the biome across a spatial domain). The geometry of rasters is described in terms of their extent (what are the boundaries of the data?), resolution (what is the size of an individual grid cell?), and projection (what coordinate system is used to describe the spatial relationship between cells?). To allow accurate calculation of isoscapes, raster data must be processed so that each of these properties is uniform across all data sets.

Finally, many isoscapes models require spatially distributed observations of isotope ratios as input or for calibration purposes. A few outstanding spatial observation networks have produced valuable spatially resolved isotopic data sets, including several IAEA programs such as the Global Network of Isotopes in Precipitation and Rivers, the US National Oceanic and Atmospheric Administration’s Cooperative Air Sampling Network, and the US Geological Survey’s North American Stream Quality Accounting Network. In a few cases, significant, spatially extensive (although temporally limited) data collections have resulted from the investigator-driven research (*e.g.*, Longinelli and Selmo 2003, Bowen *et al.* 2007), but in most cases, a high degree of coordination among multiple investigators is needed to obtain, analyze, and manage such data sets. A general lack of networked observation programs for isotopes places unfortunate limits on the availability of data that could greatly advance the quality and scope of isoscapes for migration research.

## C. Model Calculations

Following model selection, calibration, and data assembly, a provisional isoscape is created by executing the model calculations on a spatial grid using spatial data input layers. In most cases, this procedure is simply that of iteratively executing a set of calculations that solve the model equations at each grid cell in the spatial domain. Model calculations thus require a computational routine that iterates through the cells, reads data for that cell from the required data rasters, executes the model calculations, and outputs the result to a new output raster. These functions can be accomplished through hand-coded routines consisting of iterative loops, file input/output statements, and mathematical operators written in any programming language that supports these functions (*e.g.*, BASIC, FORTRAN, C, C++, Java). They can also be implemented in most commercial GIS software packages (ArcGIS, GMT, GRASS, GrADS, SURFER) that provide much of the basic functionality needed to execute these routines in the form of prebuilt tools that accomplish many of the lower-level functions (*e.g.*, reading a raster data file or iterating through the spatial grid) transparently. In many cases, this can increase the efficiency of the calculation and routine-building process, and because the GIS tools are typically available through graphical user interfaces, it allows isoscape calculations to be conducted by researchers having little or no computer programming experience.

In addition to the actual process of model execution, important decisions must be made at this step about the extent and resolution of the isoscape that will be generated: how large an area will be modeled and at how fine a spatial division? The question of extent may be one that is answered largely by practical constraints, for example, the aerial coverage required to encompass the likely range of a migrant population or the extent of a requisite geographic data set. In making decisions about the spatial extent of modeling, however, it is important to consider the extent of any calibration data that were used and critically assess whether they are sufficient to support application of the isoscapes model at the desired extent or whether unwarranted extrapolation will be involved.

Decisions about the spatial resolution at which model calculations are applied are in many cases more subjective but are equally important. A number of factors must be considered in the selection of an appropriate spatial resolution for a particular isoscape and ecological application. Biological factors, for example, the size of an individual's range on the breeding or wintering grounds, will be relevant to determining the maximum resolution that is appropriate for a particular application. In a more general sense, the number, density, and geographic specificity of calibration data will have a strong influence on the degree of spatial specificity that is appropriate for the modeling work. In this regard, it is important for both modelers and isoscapes users to recognize that higher spatial resolution is not necessarily better. In many cases, attempts to predict isotope distributions at very high spatial resolutions may actually compromise the overall quality of the resulting data products because the resolution at which the calibration and calculation work is conducted may exceed that of the physical spatial processes determining isotopic variability and introduce artifactual or overspecified dependence of the predicted isotope ratios on model variables. There is some evidence that this may be the case for some published high-resolution isoscapes of precipitation isotopic composition (Chapter 5).

## D. Optimization of Residuals

Models, as simplified descriptions of the processes they represent, inevitably fail to make perfect predictions. This is true for isoscapes models that are often limited in their complexity by the availability of spatial input data that would allow their application over the spatial scales of interest. Mismatch between the model predictions and observational data, or model residuals, can often be partly attributed to uncertainties in the data or the model parameters, but may carry important information about the inadequacies of the model. Where spatial data sets documenting the isotopic values of interest at points within the modeling domain are available, isoscape modeling offers two powerful ways to take advantage of residuals in order to optimize the end data product.

First, examination of model residuals can often produce insight into the model through comparison with ancillary data sets, leading to iterative improvements in the modeling. The residuals can be considered test cases, and mismatch with the observational data may highlight missing processes that could be incorporated to improve future modeling. GIS software facilitates the comparison of residual values with the wide range of available spatial data by allowing users to intersect and extract data at specified locations from multiple data sets: for example, residual values from a network of isotope-observing sites could be referenced against data showing land use categories to produce a spreadsheet. comparing these data across all sites.

Second, in many cases, residual values are nonrandomly distributed in space. This spatial autocorrelation presumably reflects a location-dependant process that was incompletely represented in the model, and analysis of residual spatial patterning can itself offer insight into missing model processes. Spatial autocorrelation offers another avenue to improving isoscape accuracy, however, through the use of a geostatistical interpolation model. The geostatistical model can be applied to interpolate a grid of predicted residual values that can be added to the isoscape model predictions to "correct" them against the observational data. An early analysis of precipitation isotope ratios by Bowen and Wilkinson (2002) illustrates the use of spatially autocorrelated residuals (Figure 4.3). In this case, spatially patterned residuals suggested that aspects of the climatology and atmospheric circulation not represented by the derived isoscape model used in the study had a significant impact on precipitation isotope ratios.

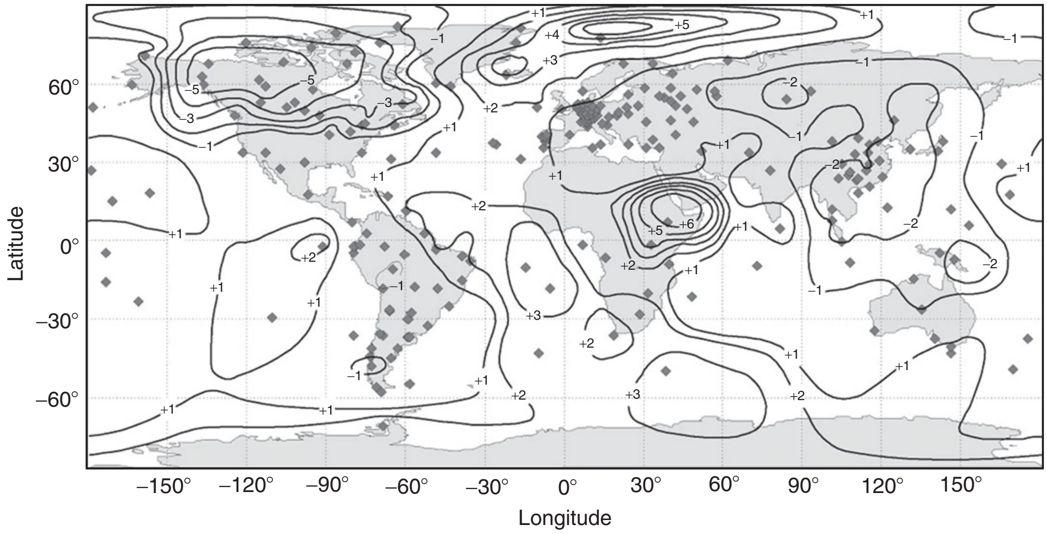

**FIGURE 4.3** Model residuals ($\delta^{18}O$, ‰) for an isoscape predictions of long-term, mean annual precipitation isotopic composition (reprinted from Bowen and Wilkinson 2002). Residual values were calculated as observed values—model predictions at precipitation monitoring sites. Low residuals values over the northern hemisphere continental interiors can be attributed to the extensive rainout of $^{18}O$ as air masses traverse the continents. High residuals over the mid- and high-latitude oceans can be attributed to extensive evaporation from the warm surface waters of the gyres in these regions. The large magnitude positive residuals in eastern Africa reflect a combination of factors including proximity to Indian Ocean water sources, reevaporation of falling rain, and relatively low decrease of isotopic values with elevation in this region.

This information could be used to develop an improved model parameterization that incorporated these environmental factors, or, as was done in the cited study, to develop a residual correction using geostatistical interpolation.

## E. Uncertainty of Isoscape Predictions

As we have shown, isoscapes are commonly the product of multilevel modeling efforts involving derived spatial data products, imperfect model parameterizations, and geostatistical analysis. Developing quantitative measures of the uncertainty of isoscapes predictions represents a current and significant challenge to the robust application of these products to migration research. Prediction error defined as the difference between an isoscape prediction at a given site and the true value of the modeled variable is itself spatially variable, and so the most useful data products documenting uncertainty are maps of standard errors, confidence intervals, or related statistics across the modeling domain. Relatively few such maps have yet been presented in the literature (*e.g.*, see Bowen and Revenaugh 2003). It is important to note that prediction error as discussed here represents only one component of error affecting ecological interpretations developed using isoscapes. Selection of appropriate isoscapes for application to a particular question (*e.g.*, annual average vs seasonal precipitation; Bowen *et al.* 2005) and development of accurate models for the relationship between tissue isotopic composition and that of the environmental substrates modeled by isoscapes are important sources of uncertainty that are beyond the scope of this chapter.

Prediction error can be partitioned into error from two sources: data error and model error. Sources of error in the data products used to calibrate, drive, or optimize spatial stable isotope models can be related to the handing and analysis of individual samples (*e.g.*, evaporation of water from improperly stored samples prior to H and O isotope ratio analysis), lack of homogeneity within large data sets (*e.g.*, using data having uneven temporal coverage to estimate long-term average isotopic values), or the generation of derived data products (*e.g.*, errors in climate model reanalyses or interpolated climate rasters). Model errors relate to the parameterization of natural processes used for modeling and the inaccuracies in these parameterizations. For example, maps of precipitation isotope ratios were produced by Bowen and Wilkinson (2002) using a fixed coefficient for variation with altitude [parameter *c* in Eq. (4.4)] at all sites, a simplifying and inaccurate assumption that biased predictions in parts of East Africa. The distinction between data and model error is often blurred in isoscapes modeling because many of the data products used are themselves model-derived.

Several methods are available for quantification of isoscapes prediction uncertainty, all of which provide accurate assessment of data error but may incompletely represent model error. Metrics of error can be derived from the covariance matrix in kriging or through error propagation (assuming estimates of parameter and variable uncertainties are available) in process-based and derived-parameter models. Resampling statistics (*e.g.*, cross-validation, jackknife, and bootstrap methods; Wu 1986) can also be applied to generate estimates of uncertainty in any of these cases, and while these methods are computationally intensive they have the significant advantage of being insensitive to assumptions about probability distribution functions and covariance functions of model parameters (*i.e.*, they are nonparametric methods). Each of these methods will quantify error associated with noisy data by calculating its impact of the precision with which model parameters are known. Model error, however, will only be adequately represented where data are available to document its impact on the precision of the model. In the case of East African precipitation isotope ratios given above, for example, the subsequent error analysis of Bowen and Revenaugh (2003) was able to identify high uncertainty for estimates in this region based on the data from a monitoring station in this region (Addis Abba). In the absence of local data, however, the inability of the fixed altitude effect parameterization to correctly predict isotope ratios in this region would not have been recognized. In such cases, the only clear routes to improving isoscape models and the estimation of error are through the parallel paths of expanded spatial data collections and improved model parameterization.

## V. ISOSCAPES FOR TERRESTRIAL MIGRATION RESEARCH

In this final section, we review many of the currently available isoscapes data products as they relate the study of terrestrial animal migration.

### A. H and O Isoscapes

Isoscapes of H isotopes in water, particularly in precipitation, have been widely applied in migration research based on the premise that the dominant source of hydrogen in body tissues is environmental water, either consumed directly or routed through diet (*e.g.*, Chamberlain *et al.* 1997, Hobson and Wassenaar 1997, Norris *et al.* 2004, Bearhop *et al.* 2005). Analogous application of O isoscapes has been investigated in at least one case (Hobson *et al.* 2004), but so far has shown less promise. The most commonly referenced products are maps of long-term average growing season precipitation isotope ratios (Figure 4.4; *e.g.*, Meehan *et al.* 2004, Bowen *et al.* 2005) produced by derived-parameter modeling of monthly data with geostatistical residual correction. These products are freely available on the web, and although uncertainty estimates specific to the growing season products have not been produced, confidence intervals generated for related annual average precipitation isoscapes (Bowen and Revenaugh 2003) provide a general indication of the potential error in the growing season maps.

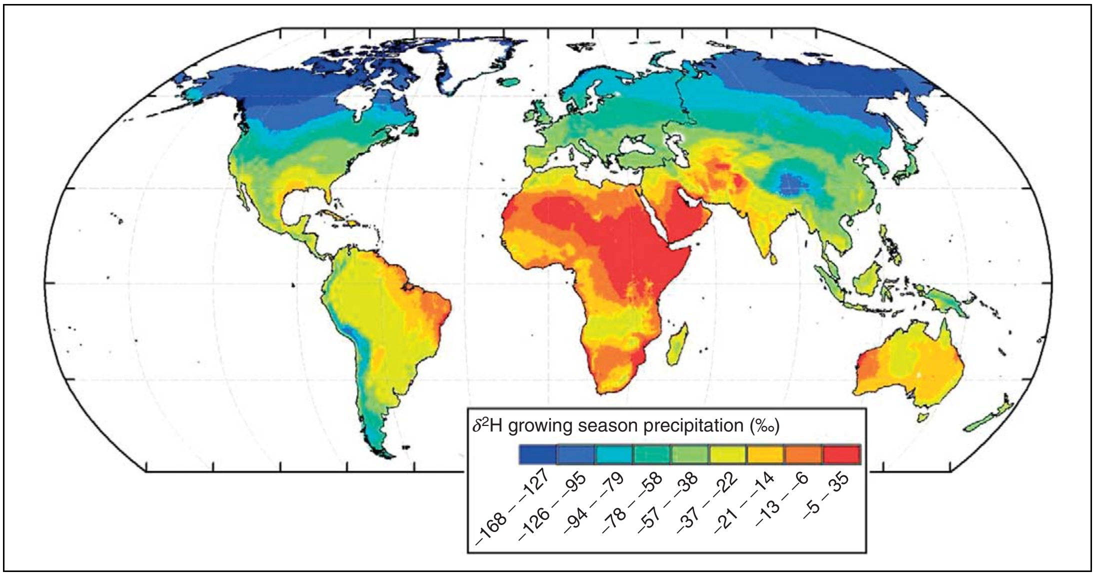

**FIGURE 4.4** Global isoscape of long-term average growing season precipitation $\delta^2$H values (after Bowen *et al.*, 2005). This map represents the precipitation amount-weighted average of monthly isoscapes produced using a derived parameter model [modified version of Eq. (4.4)] and interpolated residual correction. Climate data (temperature and precipitation) was interpolated from the Global Historical Climatological Network (Peterson and Vose 1997).

The nature and extent of isotopic variability across these isoscapes has been reviewed by Bowen *et al.* (2005). In general, they provide the greatest power to constrain the location of migration endpoints and pathways within the northern hemisphere continental interiors, and in some cases may also be useful for differentiating habitats along altitudinal gradients.

One of the greatest limitations of currently available precipitation-based isoscapes is their limited temporal specificity. In order to achieve high levels of accuracy in precipitation isoscape modeling, it has thus far been necessary to work with long-term average data accumulated over many decades of monitoring and measurement. Although the use of large, long-term average data sets greatly increases the accuracy of long-term average precipitation isoscapes (Bowen and Revenaugh 2003), it is not clear how closely these predictions reflect the environmental isotopic signal taken up by migrant individuals that inhabit a location for a period of weeks or months during a particular dry or wet year. Assessment of the variability of precipitation isotope ratios among multiple years at given sites is not a simple task, given the inconsistent and often severely limited temporal coverage of currently available data, but is needed in order to better understand the impact of year-to-year variability on the precision of interpretations made using precipitation H and O isoscapes. A similar challenge exists with respect to the seasonal specificity of these isoscapes. The rationale for restricting the data used to the "growing season" (*e.g.*, defined as all months with mean temperature >0 °C) has been that water assimilated by plants and entering the food chain will be primarily derived from growing-season precipitation, but other seasonal or annual isoscapes may be more relevant in some cases (*e.g.*, Bowen *et al.* 2005). In this case, analysis and maps of the intra-annual variability in precipitation isotopic composition are available to document the potential effects on applications to migration research (Bowen in review).

For some migratory birds and animals, H or O isoscapes of precipitation may be a poor choice for isotope tracking work, and in these cases, a new generation of isoscapes representing other water sources may improve and expand the use of water isotopes in migration research. Isoscapes of surface (river) water (Fekete *et al.* 2006) and human tap water (Bowen *et al.* 2007) have now been produced for the contiguous United States, and may be relevant to tracing some migrants, for example, with aquatic habits or that might be known to feed primarily in irrigated agricultural habitats. These products have been developed using precipitation isoscapes to represent the isotope flux to the land surface and modeling the modification of this signal using hydrological (surface water) or geostatistical (tap water) models. The first-order patterns of these isoscapes are similar to those of precipitation, but the surface and tap water isoscapes demonstrate significant differences relative to precipitation products particularly in mountainous regions and along the course of large, mountain-fed rivers. Estimates of the accuracy of these products are preliminary, but comparisons of the river water product of Fekete *et al.* (2006) to river water monitoring data suggests that the significant errors that exist could be corrected using residual interpolation to produce a river water H isoscape of relatively high accuracy.

## B. Vegetation C Isoscapes

Carbon isotope ratios have been primarily applied to studies of animal diet, largely because of the distinct isotopic signal associated with the relative proportion of $C_3$ versus $C_4$ plants in the diet (MacFadden and Cerling 1994, Cerling *et al.* 1997a,b, Sponheimer and Lee-Thorp 1999, Peters and Vogel 2005). They have not been as widely used to study migration (aquatic organisms being an important exception to this), perhaps due to disagreement in the literature over the utility of $\delta^{13}$C in yielding geographic information (Chamberlain *et al.* 2000, Wassenaar and Hobson 2001, Hobson *et al.* 2003). Vegetation $\delta^{13}$C isoscapes have significant potential to provide important insights by allowing one to compare, for example, spatially distributed data with continuous grid predictions or by providing an interpretation platform for bird feathers produced in different but unknown locations. Significant spatial information may therefore be found from model predictions that incorporate not only the distribution of $C_3$ and $C_4$ plants but also the comprehensive isoscapes that include these distributions as well as the climatic responses. By combining models of $C_3$ versus $C_4$ plant distributions, biophysical models of plant carbon isotope fractionation, and biome distributions derived from satellites to allow biome-specific plant physiology to be incorporated, global plant $\delta^{13}$C isoscapes have been produced (see Figure 4.5; Lloyd and Farquhar 1994, Scholze *et al.* 2003, Suits *et al.* 2005). These plant $\delta^{13}$C isoscapes provide a useful framework for understanding observed spatial information in bird tissue $\delta^{13}$C (Pain *et al.* 2004), assuming one understands the relationships between birds and their food source. It is of course necessary also to have some confidence in the relationship between the isoscape prediction and the actual food source (*e.g.*, if the model predicts leaf $\delta^{13}$C and the bird eats primarily seeds, what is the relationship between seed and leaf $\delta^{13}$C?). If these variables can be understood, plant $\delta^{13}$C isoscapes offer the potential for sophisticated interpretations. Greater exploration of these interfaces is clearly warranted.

## C. Vegetation N Isoscapes

Although mapping spatial variation in plant $\delta^{15}$N has received less attention than has plant $\delta^{13}$C, there is at least one published set of global plant and soil $\delta^{15}$N maps (Amundson *et al.* 2003). This modeling effort was based on prior arguments that plant $\delta^{15}$N is related to the residence time of N in an ecosystem or N cycle "openness," as well as empirical observations consistent with this expectation that plant $\delta^{15}$N is negatively correlated with precipitation (*e.g.*, Austin and Vitousek 1998, Handley *et al.* 1999). Temperature is also positively correlated with plant $\delta^{15}$N values and this relationship is part of the model by Amundson *et al.* (2003) (see Figure 4.6). It has also been observed that animal $\delta^{15}$N is negatively correlated with precipitation, a pattern that could be caused by both changes in dietary $\delta^{15}$N or animal metabolism. Recent work suggests that the pattern is the result of variation in dietary $\delta^{15}$N and not variation in animal metabolism indicating that animals (in this case, kangaroos)

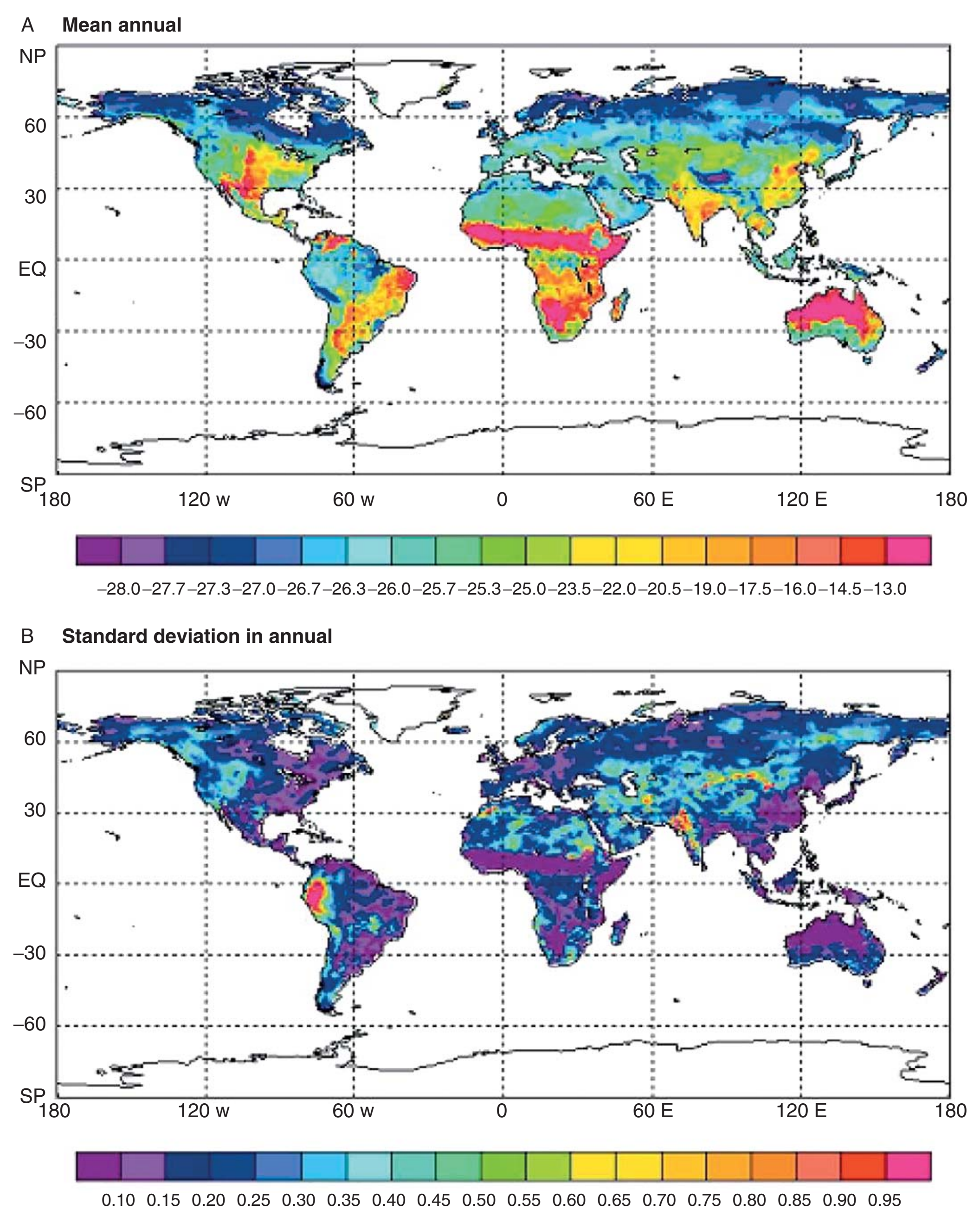

**FIGURE 4.5** Global mean (A) and standard deviation (B) annual plant $\delta^{13}$C (‰). These plant carbon isoscapes are hybrid products derived from global distribution maps of C3/C4 vegetation (derived from satellite products and physiological modeling) and modeled physiological responses of C3 plants to atmospheric conditions for the years 1983–1993 (continuous fields from ECMWF) and constrained by the Normalized Difference Vegetation Index for those years. Figure reproduced with permission from Suits *et al.* (2005).

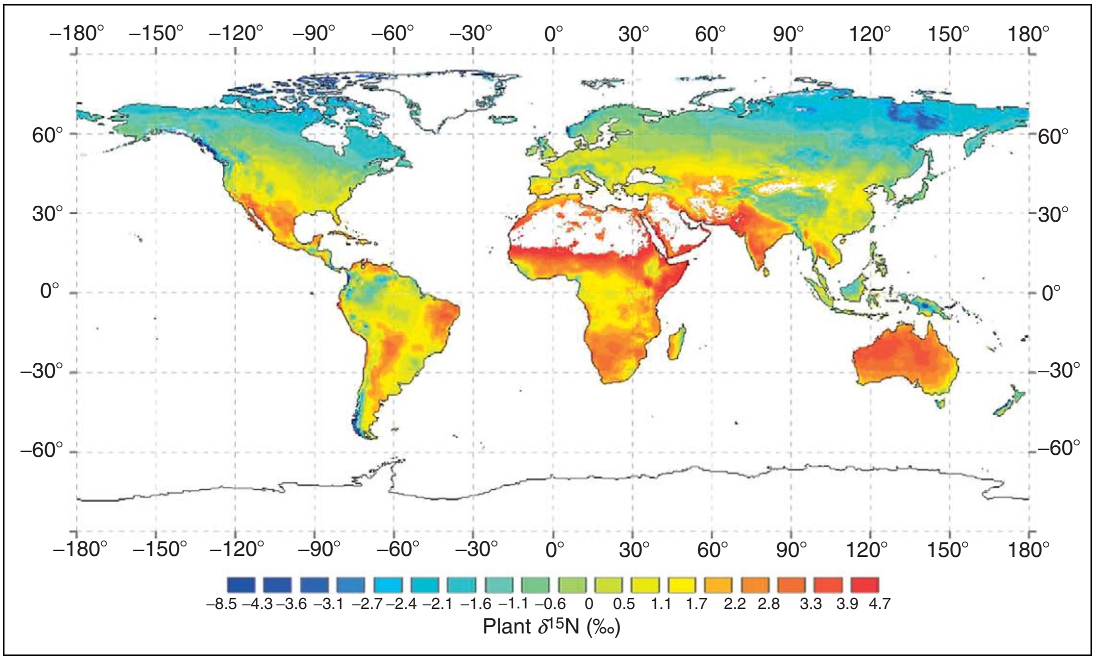

**FIGURE 4.6** Global plant $\delta^{15}$N. This plant nitrogen isoscape was produced by executing a regression model in GIS previously fit to observed plant $\delta^{15}$N and mean annual precipitation and temperature (Amundson *et al.* 2003). The model was driven with observed climate parameters (continuous fields of Mean Annual Precipitation and Mean Annual Temperature for the climate normal period 1961–1990 from the Climate Research Unit; New *et al.* 2002). The model output was further masked using continuous vegetation fields (DeFries *et al.* 1999) eliminating areas with greater than 80% nonvegetated ground.

faithfully record dietary $\delta^{15}$N and that dietary $\delta^{15}$N is itself linked to climate, likely through its effect on N cycle openness (Murphy and Bowman 2006). Support for retention of this geographic signal has also been found for warblers (Chamberlain *et al.* 2000). As with carbon, however, explicitly incorporating plant $\delta^{15}$N isoscapes into the study of animal migration remains largely unexplored and should provide important insights as these efforts increase.

## D. Vegetation H and O Isoscapes

Because hydrogen and oxygen are found in plant organic compounds and water, both plant water and organic isoscapes have been produced for application to understanding biosphere–atmosphere interactions, and others such as to commerce or forensics (see Figure 4.7; Farquhar *et al.* 1993, Ciais *et al.* 1997, Cuntz *et al.* 2003, West *et al.* 2007). These plant isoscapes have, however, not yet been widely applied to improving understanding of migration, relying instead on strong relationships between animal isotope ratios (primarily H), and drinking water isotope ratios. It seems likely that a greater understanding of all significant sources of H and O inputs to animal metabolism would yield better predictive ability, making plant H and O isoscapes potentially useful for understanding animal movement. This is especially true for animals that obtain a significant amount of their body water from plant water. Plant $\delta^{2}$H and $\delta^{18}$O isoscapes are generally derived using a combination of approaches. Plant processes that discriminate against $^{2}$H or $^{18}$O are modeled explicitly using biophysical models of the fractionation. These models are themselves driven by parameters such as plant source water isotopic composition and climate that are either simulated within general circulation models or

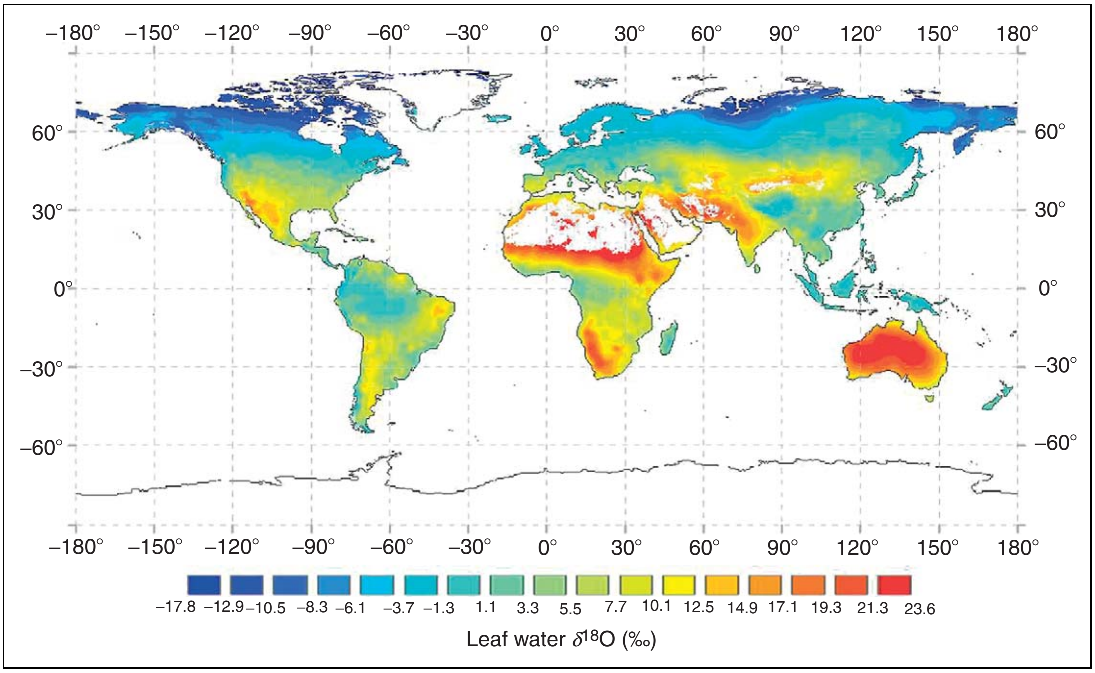

**FIGURE 4.7** Global annual average leaf water $\delta^{18}$O. This plant oxygen isoscape was produced by executing a physiological model of leaf water enrichment (modified from Flanagan *et al.* 1991) using gridded annual average precipitation $\delta^{18}$O (see Figure 4.3) and monthly climate parameters (continuous fields of temperature and relative humidity for the climate normal period 1961–1990 from the Climate Research Unit; New *et al.* 2002) to drive the model (West *et al.* in review). Monthly grids were averaged and the model output was further masked (as in Figure 4.5) using continuous vegetation fields (DeFries *et al.* 1999) eliminating areas with greater than 80% nonvegetated ground.

derived from surface water or precipitation isosocapes. In addition, the resulting plant isoscapes may be then weighted using various approaches, including maps of plant biome distributions or productivity, or simulations of the same (West *et al.* in review). Depending on the degree of understanding or available data, the plant $\delta^2$H and $\delta^{18}$O isoscapes may be general, such as a global average leaf water isoscape, or quite specific, such as a series of isoscapes depicting the changing spatial variation of leaf water for a single growing season. The degree of detail may be dictated by the availability of data or model understanding, or it may be dictated by the specificity or generality of the question being asked. As with all isoscapes discussed, the approach is flexible and not *a priori* linked to any particular temporal or spatial scale.

## E. Ecosystem Sr Isoscapes

The only published example of a large-scale Sr isoscape (Beard and Johnson 2000) represents the bedrock $^{87}$Sr/$^{86}$Sr of the contiguous United States as a function of rock age (Figure 4.8). As discussed previously, local bedrock Sr isotope ratios in many cases will be only loosely related to ecosystem $^{87}$Sr/$^{86}$Sr relevant to migration research applications (Naiman *et al.* 2000), but for large-scale, low-resolution tracking efforts, the patterns predicted by the Sr isoscape likely provide a reasonable template for first-pass interpretations. In particular, the areas of high $^{87}$Sr/$^{86}$Sr in areas of very old (Precambrian) bedrock in northern Minnesota and some Rocky Mountain states likely represent areas

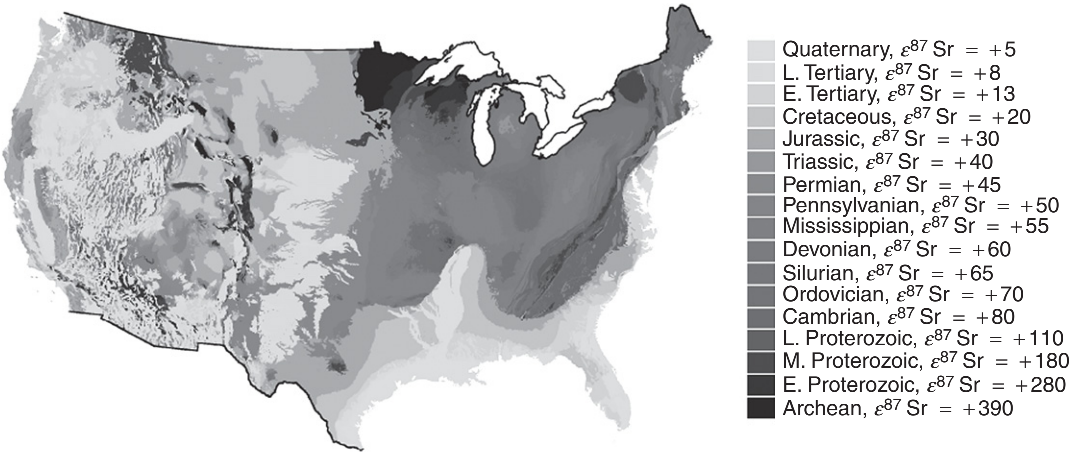

**FIGURE 4.8** Predicted $^{87}$Sr/$^{86}$Sr (as $\varepsilon^{87}\mathrm{Sr} = [(^{87}\mathrm{Sr}/^{86}\mathrm{Sr})_{\mathrm{predicted}}/(^{87}\mathrm{Sr}/^{86}\mathrm{Sr})_{\mathrm{bulk\ earth}} - 1] \times 10{,}000$) for bedrock of the contiguous United States (Beard and Johnson 2000). Values were modeled by assuming a fixed initial $^{87}$Sr/$^{86}$Sr and $^{87}$Rb and Sr content and calculating $^{87}$Sr production following rock formation using the known decay rate of $^{87}$Rb and rock ages represented on the US Geological Survey digital geological map. Reprinted, with permission, from the *Journal of Forensic Sciences*, Volume 45, Issue 5, copyright ASTM International, 100 Barr Harbor Drive, West Conshohocken, PA 19428.

where Sr isotope ratios offer power to constrain the location and habitat of migrants. Relatively low $^{87}$Sr/$^{86}$Sr mapped along the Gulf coastal plain is also consistent with the smaller-scale study of Hoppe *et al.* (1999), which, however, demonstrated additional fine structure in the spatial isotope patterning by mapping plant and rodent tooth Sr isotope ratios at sites across northern Florida and southern Georgia. The structure can largely be attributed to differences in rock type (carbonate vs siliciclastic vs igneous/metamorphic), a factor not included in the Beard and Johnson model but which could be incorporated in improved Sr isoscapes models. In regions where atmospheric deposition has been identified as an important mechanism of Sr addition to the landscape, Sr isoscapes might also be improved by basing predictions on measurements of dust $^{87}$Sr/$^{86}$Sr rather than predicted local bedrock values (Naiman *et al.* 2000).

## VI. SUMMARY AND LOOK FORWARD

The current generation of isoscapes represents an attempt to reproduce the natural fingerprint of stable isotopes on the landscape by synthesizing geospatial data and models representing the processes underlying spatial isotopic variation. The organization of these processes in the natural and anthropogenically modified environment produces patterns of spatial variation that differ among isotope systems and substrates. Each of the isotope systems discussed here (H, C, N, O, Sr) as well as the sulfur isotope system is characterized by some level of known spatial variability and thus presents opportunities for application to migration research. The greatest potential for precise tracking of migratory connectivity using isotopes may exist where combinations of discrete and continuous variation occur at nested spatial scales. Isoscapes are produced using models and data of varying complexity and specificity. All of these models and data are imperfect and accurate estimates of prediction uncertainty and continued improvements in data and models are needed to advance the scope and quality of isoscapes data products available to migration researchers. Moreover, data products having greater specificity with respect to substrate (*e.g.*, lake vs river vs precipitation water isoscapes; leaf water isoscapes for different plant types) and spatiotemporal domain are needed to reduce the reliance of migration researchers on generalized products that may be of limited (and poorly known) relevance to their system of study.

The development and testing of isoscapes models is an exciting and new area of research, and improvements in these models can be expected as research in this field advances in the coming years. In contrast, new efforts in at least two key areas will be needed to improve the quality and availability of isoscapes data products for migration research. First, the quality of all isoscape predictions is dependent at some level on the availability of spatially distributed isotopic data. Whether used only for model calibration or as input to geostatistical models, the quality and coverage (*e.g.*, spatiotemporal, physiographic, and climatological) of this data is critical to assuring the accuracy of isoscapes data products. Continued and renewed effort to collect regular, spatiotemporally distributed isotopic measurements of relevant environmental substrates is a critical area of need for the advancement of isoscapes modeling. These efforts require coordinated sampling and analysis of large numbers of samples from widely distributed locations, and are thus almost always beyond the ability of single investigators or research groups and require the coordination of national or international networks. Relatively few such programs exist, and these have generated the majority of data used for water isoscapes modeling (*e.g.*, the GNIP), and produced large data sets of atmospheric gas isotope ratios (*e.g.*, the National Oceanographic at Atmospheric Administration's Earth System Research Laboratory Global Monitoring Division). Promise for the future advancement of network-based data gathering exists in new IAEA water sampling programs for major rivers (the Global Network for Isotopes in Rivers) and atmospheric water vapor (Moisture Isotopes in the Biosphere and Atmosphere) and in efforts to develop coordinated nation-wide scientific measurement platforms in the United States (*e.g.*, the WATERS network and National Ecological Observation Network), which could provide the infrastructure and coordination for future spatiotemporal isotope data gathering.

A second area where emphasis and transformation is required is in the current model of isoscapes generation and distribution. As isoscape data products of greater specificity are sought for ecological applications, the current model of research-driven generation and distribution of static data products will no longer suffice: it will not be possible for a researcher to produce and distribute the nearly infinite catalogue of data products required for the diverse and growing array of applications. In moving forward, emphasis must shift from the sharing of data products to the sharing of models. Here, cyberinfrastructure provides a wealth of untapped opportunities. High-speed data networks, grid computing (through which computationally intensive tasks can be executed using processor resources at distributed locations), the increased availability of data on the web (including real-time satellite data), and the development of software tools that can tap all of these resources "behind the scenes" ("middleware") provide the necessary infrastructure for web portals where isoscape developers can share their models and algorithms with the broader community. If these resources are properly integrated, it will be possible to create a web resource where, for example, a migration ecologist having no specialized knowledge of plant physiology, remote sensing, or geostatistics could produce and explore isoscapes of leaf water $\delta^2$H values and their uncertainty, generated using plant physiology models, satellite data, and geostatistical analysis, for the specific spatiotemporal domains and species of relevance to his/her research project. More than any other advance, the development of such tools may promote the widespread exploration of isocapes and invigorate the testing and application of isoscapes in migration research.

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