

APPLICATION

Geographic assignment with stable isotopes in IsoMAP

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Summary

1. Stable isotope ratios of H and O ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) are intrinsic properties of biological and geological materials, and can be used to constrain the geographic origin and movements of such materials. One of the most widespread uses of such data in ecology is to reconstruct geographic movements of animals by comparing isotope ratios of chemically inert tissues to predictive models ('isoscapes') of spatial isotopic variation in environmental water.
2. Although data analysis for isotope-based geographic assignment is the subject of ongoing research, a basic framework for this work has emerged.
3. Here, we introduce and document a set of data analysis tools, implemented within the IsoMAP (Isoscapes Modelling, Analysis, and Prediction; <http://isomap.org>) cyber-GIS system, that support basic analysis of sample data for geographic assignment applications. We highlight important considerations and potential pitfalls associated with use or misuse of the tools.
4. In addition to increasing the accessibility of geographic assignment analysis, IsoMAP provides several unique capabilities related to the generation of space- and time-specific water isoscapes that may advance the field of isotope-based assignment. Functionality of the existing toolkit is limited in scope, and although the system will be actively developed in the future, it is intended to complement and not supplant more flexible and customizable analytical tools.

Key-words: stable isotopes, geographic information systems, bioinformatics, cyberinfrastructure, Web-based analysis, Bayesian statistics, migration, wildlife forensics, IsoMAP.org

Introduction

Isotope-based geographic assignment – the use of stable isotope ratios, particularly $\delta^2\text{H}$ values, of chemically inert tissues to retrospectively infer the movements of migrating animals – is among the most rapidly developing techniques in contemporary stable isotope ecology (Hobson 2011; Chabot *et al.* 2012; Hobson *et al.* 2012b; Rundel *et al.* 2013). This application uses isotopic measurements of animal tissues grown at one point in the migratory cycle and sampled at a different point to constrain the location of tissue growth. Tissue values are interpreted in the context of isoscapes, models that estimate the isotopic composition of environmental substrates that are elemental sources to food webs and exhibit strong, spatially structured variation. To the extent that consistent relationships between these environmental substrates and sample tissues exist and are known, sample origin and patterns of migratory movement can be inferred.

A range of data analysis approaches have been applied to geographic assignment problems in recent years, and several

common elements have emerged. Among these are (i) the need for accurate water isoscapes and a (ii) a widely used semi-parametric Bayesian framework for incorporating information on isotopic fractionation and variability. Recognizing the potential utility of standardized accessible tools for use in isotope-based geographic assignment analyses, we recently developed and released a set of assignment tools as a component of a broader cyberinfrastructure-supported Geographic Information System (cyber-GIS), IsoMAP (<http://isomap.org>; Bowen *et al.* 2012b). In short, IsoMAP is a Web-accessible system that provides data resources, analytical tools, and a secure user-account-based workspace for project development, documentation and archival. In addition to developing content, users can also 'publish' their projects, making these accessible and reusable by other users. The goal of this application note is to introduce and provide documentation and guidance related to the IsoMAP geographic assignment workflow (Fig. 1). We first describe the logical framework on which IsoMAP geographic assignments are based, then describe the two major components of the workflow and provide guidelines for their use and finally discuss the uses, limitations and future of the IsoMAP assignment tools.

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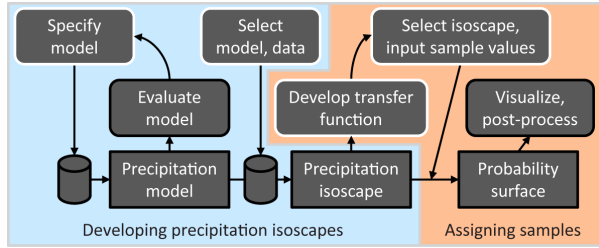


Fig. 1. Suggested workflow for geographic assignment analysis in IsoMAP. Rounded squares indicate user actions, squares are IsoMAP data products, and cylinders are IsoMAP data bases. Users can enter the workflow at any of the steps outlined in white. Workflow components in the blue and orange zones are discussed in the text subsections corresponding to the titles at the bottom of the figure.

Analytical framework

Geographic assignment analysis in IsoMAP follows a semi-parametric Bayesian framework established and applied in many recent migration studies (Wunder *et al.* 2005; Wunder 2010). Application of Bayes theorem to evaluate the probability A_i that site i is the true location of origin for a sample with measured isotopic composition δ_s yields:

$$P(A_i|\delta_s) = \frac{P(A_i)P(\delta_s|A_i)}{\sum P(A_i)P(\delta_s|A_i)}, \quad \text{eqn 1}$$

where $P(A_i)$ is the prior probability associated with location i and the summation is across all possible locations of origin (e.g. Wunder *et al.* 2005). IsoMAP's current implementation does not allow for specification of informative priors [i.e. $P(A_i)$ is assumed uniform across all locations and has no influence on the posterior probability], although as discussed below these can be incorporated during offline post-processing of results. The crux of the analysis is evaluation of the probability of observing the measured sample isotope composition δ_s at location i , which can be estimated based on predicted environmental isoscape values, information on isotopic effects associated with transfer of isotopes from the environment to the sample material and estimates of the variance (uncertainty and inherent variability) associated with these factors (Wunder *et al.* 2005; Wunder & Norris 2008; Wunder 2010; Hobson *et al.* 2012a).

For H and O isotopes where environmental water is the dominant source to animal tissues, we can assume that values of δ_s at a given geographic location are related to precipitation isotope values by:

$$\delta_s = f(\delta_p) + \varepsilon, \quad \text{eqn 2}$$

where δ_p is the precipitation isotope value at the location of sample origin and ε is a normally distributed error term with a mean of zero and variance σ_ε^2 . For almost all applications, the function $f(\delta_p)$ must be evaluated based on empirical data, either from field collections of known-origin samples or experiments with captive animals [although some semi-mechanistic models have been developed and may be relevant to a limited

subset of cases (e.g. Ehleringer *et al.* 2008; Bowen *et al.* 2009)]. In general, these relationships are found to be first-order linear, and the functional form $f(\delta_p) = \beta_0 + \beta_1\delta_p$ is adopted. This yields:

$$P(\delta_s|A_i) = \frac{1}{\sqrt{2\pi\sigma_i^2}} e^{\left(\frac{-(\delta_s - (\beta_0 + \beta_1\hat{\delta}_{p,i}))^2}{2\sigma_i^2}\right)}, \quad \text{eqn 3}$$

where $\hat{\delta}_{p,i}$ is the isoscape-predicted precipitation isotope value at site i and σ_i^2 is the total variance on the predicted sample value for site i .

Estimation and evaluation of σ_i^2 is the subject of ongoing work (Wunder & Norris 2008; Wunder 2010; Hobson *et al.* 2012a). A range of approaches have been adopted from simple estimation of bulk variance based on empirical data from known-origin samples to hierarchical modelling of component contributions associated with factors such as precipitation isotope variance, inter- and intra-individual variance attributable to behavioural and physiological factors and mass spectrometric measurement uncertainty. For IsoMAP applications, we recognize that eqn 2 implies two distinct components of variance on δ_s : (i) a spatially varying component $\sigma_{p,i}^2$ associated with precipitation isoscape estimates ($\hat{\delta}_{p,i}$) and calculated as a component of the IsoMAP precipitation isoscape modelling process and (ii) a spatially invariant component σ_ε^2 associated with all processes linking precipitation values to a measured sample value and specified by the user. Within IsoMAP, we assume independence of these components, such that for the linear model described above $\sigma_i^2 = \beta_1^2\sigma_{p,i}^2 + \sigma_\varepsilon^2$. We note that the assumption of independence will often be invalid if ε is evaluated based on empirical, known-origin data sets where precipitation isoscape data are used to estimate δ_p in eqn 2 and variance in ($\hat{\delta}_{p,i}$) is interactive with ε . In these cases, IsoMAP will in general overestimate σ_i^2 , providing a 'conservative' analysis that reduces the apparent power of the method and may lead to type 2 errors in subsequent analyses.

User workflow

DEVELOPING PRECIPITATION ISOSCAPES

The starting point for all assignment analyses in IsoMAP is selection of an isoscape describing the estimated spatial distribution of $\delta^2\text{H}$ or $\delta^{18}\text{O}$ values in an environmental substrate (Fig. 1). This can be either a custom data product produced by the user or a published product already existing within IsoMAP. At present, the system only allows the generation of precipitation water isoscapes, however, we anticipate that by the time this note is published, users will also be able to generate isoscapes estimating values for water in plant leaves. Precipitation isoscapes in IsoMAP are developed from statistical and geostatistical models that describe water isotope variation in terms of geographic location and one or more independent variables. The databases, workflow, model algorithms and source code underlying precipitation isoscape modelling in

IsoMAP are described elsewhere (Lee *et al.* 2011; Bowen *et al.* 2012a,b) and here we focus mainly on practical information related to this step in the assignment workflow.

Precipitation isoscape development in IsoMAP is a two-step process, requiring the user to first develop and optimize a model based on isotope monitoring data and secondly, apply it using gridded data to create the isoscape map. Model development involves specification of the spatial and temporal domains within which data will be extracted as well as selection of one or more model parameters. Data (both isotopic and predictor variable values) specified by the user selections are extracted from a catalogue of geospatial data resources maintained by IsoMAP, and values for each site are averaged across the specified temporal domain to obtain precipitation amount-weighted average values. These values are then used to optimize statistical (regression) and, if significant spatial autocorrelation exists in the data, geostatistical model parameters, as specified by the user's selections.

A range of geographic and environmental variables (e.g. temperature, precipitation amount, elevation), and data sources for these variables are made available to users, and no universal guidelines can be provided for variable selection. Known relationships and causal links between many of the IsoMAP variables and precipitation isotope ratios are discussed extensively in the literature (e.g. Rozanski, Araguas-Araguas & Gonfiantini 1993; Bowen, Wassenaar & Hobson 2005; van der Veer *et al.* 2009; Bowen 2010a,b). These papers offer an excellent starting point for model developers. IsoMAP also provides extensive statistical output for all models, including values such as AIC and cross-validation errors that can be used to directly compare alternative models. Our recommendation is that new users explore and compare a range of models that may be relevant to their system of interest before proceeding with their analysis.

Any precipitation isoscape model developed within IsoMAP can be used to produce maps of predicted isotope values and the uncertainty therein. The primary user-input step in this process is the selection of gridded data sources from which the independent variable values required by the model are obtained. Depending on the selected temporal and spatial domains, one or more data sources may be available. These gridded data products may have differing spatial resolutions, and by default, IsoMAP will resample all products used to the coarsest resolution of the input grids. As a result, the spatial resolution of the final product produced is determined by the gridded data sources selected by the user. Although relatively high-resolution (e.g. 1×1 km) products can be obtained for some regions and models, we encourage caution when applying these products in assignment problems, given that in many cases, the actual patterns of environmental isotope variation 'experienced' by animals may be spatially attenuated by hydrological or other environmental processes.

IsoMAP offers a relatively high degree of flexibility in the production of water isoscapes. The advantage of this flexibility is that water isotope data products can be developed that are

specific to particular regions and time periods. In many cases, these may be more appropriate for use in assignment analyses than the global 'climatological' (multidecadal average) products that have been used in most published work. For example, regional models can often more accurately predict isotope distributions within given climatic zones than globally optimized models (Lykoudis & Argiriou 2007), and rainfall isotope ratios for climatically anomalous years may provide a more accurate baseline against which to compare animal tissues grown during those years (Van Wilgenburg *et al.* 2012). This flexibility can create challenges, however, in that the appropriate selection of isoscapes is not always clear-cut. Work with known-origin birds has suggested that in most cases H isotope ratios of feathers are most closely linked to the isotope ratios of precipitation falling during the growing season (e.g. Bowen, Wassenaar & Hobson 2005; Hobson 2011), but this need not be the case for all organisms or tissues. In addition, the use of custom region- or time-specific isoscapes requires that users carefully evaluate transfer functions used to describe the relationship between environmental water and animal tissue isotope values, as discussed below.

ASSIGNING SAMPLES

Once an environmental isoscape has been selected, IsoMAP requires the user to input two values representing the observed sample isotopic composition (δ_s) and standard deviation associated with the environment to sample transfer (σ_e). Because IsoMAP was designed to support water-isoscape-based geographic assignment of a wide range of sample materials (e.g. waters, animal tissues, products), the convention adopted requires that these values be input as equivalent water isotope values corresponding to the observed or estimated sample values (δ_{sp} and σ_{ep} , respectively). The expression evaluated by IsoMAP is then:

$$P(\delta_s|A_i) = \frac{1}{\sqrt{2\pi(\sigma_{p,i}^2 + \sigma_{ep}^2)}} e^{\left(\frac{-(\delta_{sp} - \hat{\delta}_{p,i})^2}{2(\sigma_{p,i}^2 + \sigma_{ep}^2)}\right)} \quad \text{eqn 4}$$

Because in almost all cases, the function $f(\delta_p)$ is linear with respect to δ_p , a mathematically equivalent version of eqn 3, posed in terms of δ_p , can be derived. For the commonly-used first-order linear case described above, we can write:

$$P(\delta_s|A_i) = \frac{1}{\sqrt{2\pi\sigma_i^2}} e^{\left(\frac{\left(\left(\frac{(\delta_s - \beta_0)}{\beta_1}\right) - \hat{\delta}_{p,i}\right)^2}{2\left(\sigma_{p,i}^2 + \left(\frac{\sigma_e}{\beta_1}\right)^2\right)}\right)} \quad \text{eqn 5}$$

Equation 5 then gives algebraic expressions that can be used to obtain the appropriate user-input values for the exponential term of the IsoMAP calculation:

$$\delta_{sp} = (\delta_s - \beta_0)/\beta_1, \quad \text{eqn 6}$$

and:

$$\sigma_{ep} = \sigma_e / \beta_1. \quad \text{eqn 7}$$

Note that the IsoMAP equation uses the rescaled version of σ_i in the pre-exponential term (i.e. compare eqns 4 and 5), meaning that the values calculated are $P(\delta_s | A_i) \times (1/\beta_1)$. Because the posterior probabilities are linearly rescaled to sum to one across all possible locations (eqn 1), however, this artifact has no impact on the resultant probability of origin surface.

To summarize the above discussion, development of probability-of-origin surfaces in IsoMAP requires that users (i) obtain estimates of the transfer function parameters and variance, for example from a regression of known-origin sample values against measured or estimated precipitation values, and (ii) mathematically rescale the sample value and transfer function variance (e.g. eqns 6 and 7) to provide appropriate values for the IsoMAP calculations.

The development and specification of the environment to sample transfer function is perhaps the most critical component of the assignment analysis, and although the release of IsoMAP's assignment toolkit is relatively recent, examples already exist in the literature, where questionable practices have likely led to erroneous results (Wittenberg, Lehnen & Smith 2013). IsoMAP allows users flexibility in transfer function development, but at least two general points should be considered. First, in almost all cases, a transfer function will be required. The isoscapes generated by IsoMAP are representative of precipitation water isotope ratios. Although this water is the ultimate source of H and O to most terrestrial biological systems, and thus strongly isotopically related to biological sample values, environmental and biological processes lead to both isotopic offsets between, and differences in local variance values for, precipitation and biological samples. Input of measured or estimated biological sample values in IsoMAP without appropriate rescaling will almost always generate bogus results.

Secondly, users should recognize that transfer functions are both organism- and isoscape-specific. Recent work has emphasized differences between transfer functions for animals of different age (e.g. Wunder 2010) or feeding guild (Hobson *et al.* 2012a), and in some cases has led to the development of transfer functions that may be of general use in studies involving certain species. In most cases, these functions have been developed using isoscape-based climatological growing season average precipitation isotope values as the independent variable. Adoption of these functions in applications where the IsoMAP isoscape being used is not closely comparable to that used in transfer function development (e.g. using an annual average or single-month IsoMAP isoscape) will produce errant results. We echo the recommendation of other authors that the best approach to this problem is to develop transfer functions that are specific to the study organism and isoscape being used, that is, via comparison of measured values for widely distributed known-origin individuals with the environmental isoscape. In applications where this is not possible or where for other

reasons a generic transfer function is used, we encourage users to carefully evaluate the comparability of the isoscapes used in calibration and assignment: they need not be identical, but should provide a consistent representation of the environmental isotope patterns that are expected to control sample isotope values.

BATCH ASSIGNMENT

Most assignment applications will involve the independent assessment of the geographic origins of individuals, possibly leading to subsequent summaries that attempt to draw conclusions about groups of individuals. IsoMAP currently supports one special-case application of group inference. In cases where the sampled individuals are known or assumed to represent a single population with a shared geographic origin, the individual sample values can be considered to be independent samples from the distribution given by eqn 2. The IsoMAP batch assignment tool allows users to input n values representing such a set of samples and uses them to calculate a map of joint probability-of-origin values that may give a more precise estimate of group origin than do the individual sample assignments. Equations 3 and 1 are evaluated for each location in the spatial domain and each sample, producing n probability surfaces. These are then multiplied to obtain a joint probability or likelihood value, for each map grid cell. These values are rescaled to sum to 1 across the map domain. We stress that this mode of analysis is only appropriate for samples truly drawn from a single 'geographic' population and point users to Wunder (2010) for a discussion of potential pitfalls associated with inappropriate use of such methods.

Output and post-processing

Output from IsoMAP jobs is stored as a suite of metadata and results files that are associated with a unique job number, stored on IsoMAP's secure data system and indexed in IsoMAP's searchable jobs data base. Users can download output files for their jobs in a compressed archive, which also contains a readme file describing the archive's contents. In addition, users can find, visualize and download results from other users' jobs if those jobs have been published within IsoMAP (accomplished through IsoMAP's job management page). The IsoMAP citation policy requires that any jobs used in published work should also be published within the IsoMAP system and the relevant job numbers reported, ensuring the traceability of the user's results. IsoMAP also provides basic visualization tools that allow users to view and query maps within a Web GIS window.

Output from geographic assignment jobs consists primarily of gridded map files reporting probability of origin values (eqn 1) for each grid cell in the map domain. These files are provided in two standard formats (geotiff and ascii text, the latter with a header formatted according to conventions used by ESRI's ArcGIS software). Depending on the precipitation isoscape product used, either one or two maps may be generated, reflecting analyses based on the statistical and/or geostatistical

precipitation isoscape models. Although a detailed discussion is beyond the scope of this note, there is a substantial and growing literature discussing various approaches to analyzing and interpreting the probability surfaces in the context of specific ecological or management questions (e.g. Wunder & Norris 2008; González-Prieto *et al.* 2011; Kennedy, Bowen & Ehleringer 2011).

By downloading and post-processing assignment job results, users can extend their analysis to incorporate external information not currently supported within IsoMAP. For example, IsoMAP limits users to the selection of spatial domains that are rectangular in latitude/longitude space, whereas in many cases, the relevant spatial domain might be well known and irregularly shaped (e.g. where species range maps are available; Van Wilgenburg & Hobson 2010). Application of masks to the IsoMAP data products and rescaling of the posterior probabilities (i.e. to restore the summation to unity) can be performed in standard GIS software or within programming environments such as R. Similarly, where informative prior probabilities are available, these can easily be multiplied with the IsoMAP-output values on a gridcell-by-gridcell basis, and the resultant values rescaled following eqn 1.

Caveats and limitations

Our goal in developing IsoMAP was to provide accessible, standardized tools for the spatial analysis of isotope data, including in geospatial assignment applications. As is the case, with any analytical tool of its type, the value of the results obtained is entirely dependent on the level of rigor applied by the user. In this note, we have attempted to provide documentation and key guidelines regarding the use of the IsoMAP assignment tool, but we encourage any user to carefully review the literature surrounding this class of applications, carefully and critically evaluate each step of their analysis and contact us directly if in doubt about the technical details of the IsoMAP implementation.

Given the overhead involved in developing the system, IsoMAP's assignment tools are (and will continue to be) relatively rigid, and will not fully meet many users' needs. The precipitation-equivalent variable values required by IsoMAP, for example, can easily be derived for systems where sample values are a linear function of δ_p (e.g. eqns 6 and 7), but equivalent scaling may not be possible where these relationships are more complex. In addition, recent research in areas such as fully Bayesian (Rundel *et al.* 2013) and multi-marker assignment (Van Wilgenburg & Hobson 2010; Chabot *et al.* 2012) is leading to more complex and more informative analyses that will ultimately drive the field in new directions. Our intention is to remain responsive to these developments and attempt to both refine the existing IsoMAP implementation and add new capabilities as consensus emerges around productive approaches. Among our near-term goals is an alternative batch assignment tool that outputs n individual probability-of-origin surfaces corresponding to the n samples entered by the user, increasing the range of post-processing data analysis opportunities available to users of this tool (e.g. González-Prieto *et al.* 2011). In cases where

the IsoMAP assignment tools are not appropriate for a particular analysis, the system may still be useful for generating precipitation isoscapes that can be exported and used in off-line assignment analyses.

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