

IB290 – Ancestral State Reconstruction – annotated bibliography
07 November 2019

Dobzhansky T, Sturtevant AH. Inversions in the chromosomes of *Drosophila pseudoobscura*. *Genetics*. 1938; 23(1):28.

- (Foundation/concepts)
- One of the earliest applications of ancestral state reconstruction in which the principles of ancestral state reconstruction were first outlined. Authors were trying to infer the evolutionary history of chromosomal inversions in *Drosophila pseudoobscura*.

Fitch WM. Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Biology*. 1971; 20(4):406–16.

- (Foundation/maximum parsimony)
- Early implementation of ancestral state reconstruction that utilizes the maximum parsimony approach, “Fitch’s Method”. In this method ancestral character states are assigned by traversing a rooted, binary tree, first from the tips to the root, and then vice versa.

Cunningham CW, Omland KE, Oakley TH. Reconstructing ancestral character states: a critical reap- praisal. *Trends in Ecology & Evolution*. 1998; 13(9):361–6.

- (Foundation/Methods)
- Outline the pitfalls of using Maximum parsimony to infer ancestral character states. Important to remember that in a MP approach the goal is to minimize the number of character state changes. Two of the most common assumptions in MP are that characters evolve at constant rates along a tree, and that gains and losses of traits are equally probable. This is often violated, especially when there is rapid evolution, and unequal probabilities of transitions of character states.
- Paper compares MP methods with ML and BI as alternative approaches

Schluter D, Price T, Mooers AO, Ludwig D. Likelihood of ancestor states in adaptive radiation. *Evolution*. 1997; 51(6):1699–711.

- (Foundation/Maximum likelihood)
- Classic paper that utilizes a ML approach to reconstructing ancestral states of discrete and continuous characters in model adaptive radiation systems using continuous-time Markov chains models.
- Authors show that when changes between character states are rare, than MP and ML estimates are similar. However, if changes are frequent than estimates are prone to a degree of uncertainty, especially among deeper nodes within the tree.

Yang Z, Kumar S, Nei M. A new method of inference of ancestral nucleotide and amino acid sequences. *Genetics*. 1995; 141(4):1641–50.

- (Methods/Bayesian inference)
- Development of the empirical Bayesian approach in which the tree and model of evolution is provided apriori.

Pagel, M. (1999). The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic biology*, 48(3), 612-622.

- (Conceptual/Maximum likelihood)
- Paper provides a conceptual summary of maximum likelihood approaches to ancestral state reconstruction of discrete characters and how the methods differ from parsimony approaches, using a series of simplified examples and thought experiments.

Huelsenbeck JP, Bollback JP. Empirical and hierarchical Bayesian estimation of ancestral states. *Systematic Biology*. 2001; 50(3):351–66.

- (Methods/Bayesian inference)
- Development of the Hierarchical (full) Bayesian approach to ancestral state reconstruction, in which the tree, model of evolution and character states are jointly estimated.

Huelsenbeck JP, Nielsen R, Bollback JP. Stochastic mapping of morphological characters. *Systematic Biology*. 2003; 52(2):131–58.

- (Methods/Bayesian Inference/Discrete characters)
- Outlines the flaws of using MP to map character traits on phylogenies.
- Implements continuous time Markov Chain models under a Bayesian framework that assesses co-variation between character states. Presents stochastic trait mapping as an alternative to ancestral state reconstruction, as ASR methods rely on using marginal likelihood estimates.

Brandley, M. C., Huelsenbeck, J. P., & Wiens, J. J. (2008). Rates and patterns in the evolution of snake-like body form in squamate reptiles: evidence for repeated re-evolution of lost digits and long-term persistence of intermediate body forms. *Evolution: International Journal of Organic Evolution*, 62(8), 2042-2064.

- (Applied/Discrete characters/Morphometrics/Divergence times)
- Authors used geometric data for 258 species of squamates and time-calibrated phylogeny to investigate the evolution of limb and digit loss, and body elongation. Methods include joint estimation of ancestral states, phylogeny and divergence times
- Authors found evidence for repeated loss and gains of digits, and different patterns of body elongation in burrowing versus surface-dwelling ecomorphs.
- Using a time-calibrated phylogeny the authors could also make inferences about the tempo of change. Body form transitions appeared to take place over 20-70 MY, but intermediate forms are able to persist for tens of millions of years.

Butler, M. A., & King, A. A. (2004). Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *The American Naturalist*, 164(6), 683-695.

- (Methods/Continuous Characters)
- Compares Ornstein-Uhlenbeck (OU) and Brownian models of character trait evolution using a case study of a model adaptive radiation in *Anolis* lizards.
- OU models incorporate drift and selection parameters as well as an optimal value parameter, unlike pure drift (Brownian motion) models.

Finarelli, J. A., & Flynn, J. J. (2006). Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. *Systematic Biology*, 55(2), 301-313.

- (Continuous characters/Fossil calibrations)
- Authors used body size (mass) data from 149 extant and 367 extinct taxa to reconstruct the ancestral states of the mammalian subclade Caniformia (Carnivora, Mammalia).
- ASR using only extant taxa data showed a bias towards inferring larger body size for internal nodes, while incorporating fossil data supported smaller body sizes. Discarding temporal (dating) information resulted in ambiguous ancestral state estimates, highlighting the importance of incorporating both character state and temporal information in fossil calibrations.

Olsen, A. M. (2015). Exceptional avian herbivores: multiple transitions toward herbivory in the bird order Anseriformes and its correlation with body mass. *Ecology and Evolution*, 5(21), 5016-5032.

- (Applied/Continuous characters)
- An applied paper on continuous characters. In this study the author sought to reconstruct the evolutionary history of herbivory in the Anseriformes (ducks, geese), motivated by the observation that many purely herbivorous avian species are often flightless and possess larger body sizes. The authors sought to investigate whether transitions towards a more herbivorous diet is accompanied by transitions to larger body sizes within the Anseriformes.
- Herbivory was scored by the continuous variable, the herbivory index, which is a measure that scales from 0 -1. This continuous variable was used in the ancestral state reconstruction analysis. The relationship between herbivory and mean body size for each species was assessed using phylogenetic correlation tests.
- Model testing was conducted in order to select the best-fitting model of evolution (AIC criterion) for continuous trait evolution.
- Overall the authors found multiple transitions towards a more herbivorous diet in the Anseriformes, that appeared to lack a correlation with body size.

Joy, J. B., Liang, R. H., McCloskey, R. M., Nguyen, T., & Poon, A. F. (2016). Ancestral reconstruction. *PLoS computational biology*, 12(7), e1004763.

- (Review/Discrete/Continuous)
- A relatively recent review paper that provides a nice overview of ASR methods. It includes a brief history of the ASR methodology, the differences between parsimony, maximum likelihood and Bayesian methods, and outlines the different applications of ASR with discrete and continuous data.