

Exploring and Extending Multivariate Brownian Diffusion Models
of Morphological Character Evolution in Bayesian Phylogenetic Contexts

By

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*To someone very important . . .
a nice dedication.*

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ABSTRACT

Exploring and Extending Multivariate Brownian Diffusion Models of Morphological Character Evolution in Bayesian Phylogenetic Contexts

The abstract submitted as part of your dissertation, in the introductory pages, does not have a word limit. It should follow the same format as the rest of your dissertation (1 inch margins, double-spaced, consecutive page numbering, etc.).

ACKNOWLEDGMENTS

Acknowledgements to those who helped you get to this point. They should be listed by chapter when appropriate.

Chapter 1

Bayesian Phylogenetics Under Multivariate Brownian Motion

1.1 Abstract

The field of statistical phylogenetics has progressed tremendously in recent decades. Development and application of molecular evolutionary models stand in stark contrast to limited adoption of corresponding models of morphological evolution. Given the nature of data primarily available to paleontologists — shapes and sizes of bones and teeth — insufficient exploration of morphological models has impeded statistical inference of phylogeny among fossil taxa too old for the preservation of ancient DNA. Here, we present and perform inference under a stochastic multivariate Brownian diffusion model informed by quantitative genetics to describe the evolution of continuous traits. Unlike previous work, our model explicitly accommodates non-independence among traits, which may more realistically reflect biological phenomena such as pleiotropy and developmental integration. We then explore the statistical behavior of this model through analysis of simulated data and evaluate its performance with respect to retrieving simulating phylogenetic model parameters, with particular focus on tree topology. Finally, we apply our method to an empirical dataset consisting of 57 craniometric measurements collected by William Howells on a globally distributed set of modern human populations. Posterior distributions obtained from this analysis were consistent with accepted relationships in these groups. Several extensions of this model are also in development that will allow it to flexibly accommodate a wider range of data, such as polymorphic discrete morphological traits, and join it with molecular data to better shed light on evolutionary relationships linking both fossil and extant taxa. [Statistical Phylogenetics; Morphological Evolution; Bayesian Inference; Multivariate Brownian Motion]

1.2 Introduction

Statistical phylogenetics has undergone tremendous methodological progress in recent decades (Holland 2013). Most efforts, however, have centered on the description and implementation of discrete-state continuous-time Markov chain (CTMC) models of nucleotide substitution, with comparatively little attention paid to the development of morphological evolutionary models. When genetic data are available, both paleontologists and neontologists can fit molecular phylogenetic models in their framework of choice to make inference of the phylogenetic relationships linking taxa of interest, as well as many other phylogenetic model parameters. But for inferring phylogeny, paleontologists can only make direct use of molecular phylogenetics insofar as they can obtain viable ancient DNA – degradation quickly limits the temporal depths from which taxa can be drawn (Pickrell and Reich 2014). Past those limits, they must use morphology to infer phylogeny.

Methods for inferring phylogeny using morphological characters are limited (Holland 2013, Lee and Palci 2015). Currently, both model-based and heuristic methods are commonly used. The former rely on mathematically explicit descriptions of evolutionary process and can be fitted in both Bayesian and Maximum Likelihood frameworks. For morphological characters, the most popular inference model is Lewis’ (2001) Mk-model, which is the k -state generalization of the Jukes-Cantor (1969) model of nucleotide substitution (when $k = 4$, the models are equivalent, as the state-space of DNA is 4. For discrete binaries – morphological traits that can be present or absent, large or small, and so on – $k = 2$). Here, a discrete morphological trait changes state according to a continuous time Markov process where rate is independent of current state and waiting times between transitions are exponentially distributed. Rate heterogeneity between independent traits is straightforward to accommodate (Wright et al. 2015). Further generalization can allow for non-independence between traits by specifying states as combinations of traits and unequal rates of change between those combinations, but this rapidly swells the state-space even for modest numbers of traits (e.g. 10 non-independent binaries will have 2^{10} possible states). Correctly fitting this model under maximum likelihood produces a point estimate of tree topology, branch lengths, and evolutionary model parameters that corresponds to

the parameter values under which the observed data are most probable (the Maximum Likelihood Estimate, or MLE). Conversely, in a Bayesian framework one’s target of inference is the entire joint posterior distribution of phylogenetic model parameters, often approximated with Markov chain Monte Carlo (MCMC).

However, morphological variation between groups is frequently not discrete, but continuous. While distances can easily be computed between sets of continuous characters, inference under the Mk-model (Lewis 2001) requires that we discretize any continuous observations. This discretization can be done in a variety of ways (Garcia-Cruz and Sosa 2006, Thorpe 1984) in part subject to researcher preference, with some methods discarding less phylogenetically discriminatory information than others (Brazeau 2011). But even discrete characters collected at the outset may just be discretizing some fundamentally quantitative feature (Wiens 2001), relying on a researcher’s present observations and prior experiences instead of an explicit algorithm run on the character alignment in its entirety. As such, we may desire statistical methods for inferring phylogeny that can make direct use of continuous characters without discretizing them.

Brownian motion represents a mathematically and computationally tractable description of continuous character change and can be shown with quantitative genetics and appeal to the central limit theorem to approximate a variety of evolutionary processes under a polygenic, additive model, including evolution at mutation-drift equilibrium, fluctuating selection, and constant directional selection (Weaver 2018, Harmon 2018). Briefly, consider that under polygenicity, continuous character values are binomially distributed, and when the number of loci underlying a polygenic trait is high, the normal approximation to the binomial holds (via the central limit theorem, as binomial random variables are sums of independent Bernoulli random variables, which have finite variance). Since the difference between two normal random variables is itself normal, a Brownian motion model (described in further detail below) can be a good approximation of an evolutionary process acting under the above conditions. First described empirically by Brown (1828) and mathematically by Einstein (1905), it has enjoyed considerable attention in the context of phylogenetic comparative methods (Felsenstein 1985), where it is often contrasted

with more parameter-rich Gaussian models, such as the Hansen model (Butler and King 2004, Beaulieu et al. 2012), to better understand the evolutionary processes that structure morphological variation when the tree on which the characters evolved is assumed to be known. Recently, the statistical performance of a univariate Brownian motion model has been explored through simulation (Parins-Fukuchi 2018). Here, moderate numbers of independent continuous traits contained sufficient information to reliably retrieve the simulating tree’s topological structure under varying degrees of model misspecification, though as correlation between traits increased in the simulating model so too did error under the misspecified inference model.

As phenomena such as integration, pleiotropy, linkage disequilibrium, and correlated selection are likely to structure the evolution of continuous traits (Cheverud 1996, Young and Badyaev 2006, Mitteroecker and Bookstein 2007, Klingenberg 2008, Klingenberg 2014) across a variety of taxa (e.g. Parsons, Márquez and Albertson 2011, Klingenberg et al. 2012, Neaux et al. 2018), it may not always be safe to assume each trait to be an independent realization of some univariate Brownian motion process. Moreover, explicitly working within a multivariate framework can also enable more nuanced reconstruction of both fossil (in the case of fragmentary remains – i.e. missing data) and ancestral phenotypes and permit the direct investigation of correlated evolution between traits, integrated over phylogenetic uncertainty.

Here, we describe an approach for inferring phylogeny from continuous-character data under a multivariate Brownian diffusion model that allows them to evolve non-independently. Then, we explore the statistical performance of the model and the validity of its RevBayes (Höhna et al. 2016) implementation using a comprehensive simulation study. Finally, we apply the method to well-studied empirical dataset consisting of cranial measurements collected on extant human populations (Howells 1973, 1989, 1995).

1.3 Specifications

Consult the calendar for the dates to file your thesis or dissertation at Graduate Studies. The dates are also in the General Catalog. You are responsible for observing the filing

dates and for preparing the thesis or dissertation in the proper form.

Your thesis/dissertation must be submitted via the ETD website as a single PDF file. No file compression, password protection, or digital signature are allowed.

1.3.1 Style and Format

You should be guided on matters of style by the chair and members of your thesis committee. Graduate Studies is not concerned with the form of the bibliography, appendix, footnotes, etc. as long as they are done in some acceptable, consistent and recognized manner approved by your committee.

There are many valuable references available to assist students in preparing and writing research papers and theses [?, ?, ?]. Listed below are references that have been suggested by students and faculty¹.

- MLA Handbook for Writers of Research Papers, Theses and Dissertations, by Joseph Gibaldi and Walter S. Achtert: The Modern Language Association of America, 4th ed., 1980.
- The Elements of Style, by William Strunk, Jr., E.B. White and Roger Angell: Longman, 4th ed., 2000.
- The Lively Art of Writing, by Lucile V. Payne, Mentor Books, reissue ed., 1983.
- The Chicago Manual of Style, University of Chicago Press, 15th ed., 2003.

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You will need to produce two different title/signature pages:

- A title/signature page which will include a signature line above each committee members typed name. The signature page is to be signed by all members of your committee when they have approved the thesis or dissertation. All committee members must sign the same page and only original signatures will be accepted.

¹Be sure to search the internet for additional writing resources.

- A title page with the typed names of your thesis/dissertation committee without signatures. This will be the first page of the electronic thesis/dissertation PDF file which you will submit via the ETD website. This second format is required to prevent the publication of the signatures of your committee members.

Make an appointment with your Student Affairs Officer in Graduate Studies to submit the signature page and required forms. To find your assigned Student Affairs Officer in Graduate Studies, go to the Graduate Programs page and click on your program, then click on “People.” You will find their name and contact information there.

1.3.3 Margins

Every page of the dissertation or thesis must have a one inch margin on all sides (top, bottom, left and right). However, the page number may appear outside of these margins.

Please Note: These minimum specifications also apply to all figures, charts, graphs, illustrations and appendices.

1.3.4 Spacing

Double spacing should be used in typing the thesis, except in those places where conventional usage calls for single spacing – for example, footnotes, indented quotations, tables, and the bibliography.

1.3.5 Pagination

The preliminary pages, including the title page are numbered with small Roman Numerals which are centered at the bottom of the page. Begin numbering the preliminaries in lower case Roman Numerals with the title page which is always “i”.

The text and all other pages of the thesis or dissertation, including charts, figures, caption pages, maps, and appendices are all numbered consecutively starting with Arabic “1”. These page numbers should also be centered at the bottom of the page. (In most cases, this will start with the Introduction or Chapter 1.) Do not start renumbering pages at any point in the body of your thesis or dissertation.

With the exception of the copyright page (which should not be numbered or counted in the numbering sequence), every page must be numbered consecutively and there must

be no blank pages.

1.3.6 Typeface

Consistency is essential. The same font size and style must be used throughout. Use a font size between 10 and 13 points.

Any font style is acceptable, however you must make sure all your fonts are embedded fonts. See the instructions for embedded fonts on the ETD website.

1.3.7 Paper

Your thesis/dissertation must be submitted electronically; therefore, the Office of Graduate Studies does not require you to provide a printed copy of your manuscript. However, members of your committee and/or your graduate program may require that you provide them with a paper copy. Consult with your graduate program and thesis/dissertation committee regarding printed copy requirements.

Chapter 2

The Second Chapter

2.1 Overall Appearance

You are responsible for the appearance of your manuscript in PDF. It will appear and may be downloaded exactly as you submit it.

2.1.1 Tables, Graphs and Captions

Charts and tables may be placed horizontally or vertically, but in either case must fit within the required margins. It may be necessary to use a reducing copier in order to achieve this. If necessary, wide tables, charts, and figures can be placed sideways. Figures may be embedded in the text or take up a full page. Each figure or table must be numbered consecutively (do not renumber each chapter unless you include chapter numbers, e.g., Fig. 1.1, Fig. 2.1, etc.) and should have a caption.

NOTE: If your figures or charts are placed horizontally on the page (i.e. in “Landscape” orientation), your page number must still appear in the same place as all other page numbers (centered at the bottom of the page in “Portrait” orientation). Pagination must be consistent throughout the document.

2.1.2 Photographs, Illustrations and Maps

Plates, figures, illustrations, maps and photographic reproductions must be clear and distinct. Pagination must be consistent.

2.1.3 Oversized Material

Consult the ETD website guidelines for uploading supplemental files with your manuscript.

2.1.4 Using Published Material

If approved by the thesis or dissertation committee, reports of research undertaken during graduate study at UC Davis which have been published may be accepted in printed form as all or part of the master's thesis or doctoral dissertation. If you are not the sole or first author of the published material submitted, the use of co-authored materials must be approved by the department or graduate group concerned. The pages of the published material must meet the same formatting guidelines. Each chapter may have an abstract of its own. There must be a general abstract covering the entire dissertation.

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Since the submission of your thesis or dissertation to the University Library and/or its being made available by PQIL may constitute a form of publication, you may have to obtain permission to use (or quote) copyrighted material, such as that in most journal articles or books. It is the author (i.e. you) who is responsible in the matter of copyrighted materials. The agreement, which you submit to PQIL, specifically absolves them of any such responsibility.

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2.1.6 Dates of Filing

Check the calendar for deadlines for filing the master's thesis or the doctoral dissertation with the committees in charge and with Graduate Studies. Deadlines are also announced each year in the Class Schedule and Registration Guide and the General Catalog. The deadline for filing with your committee is a recommended deadline to allow time for making revisions. The deadline for filing with Graduate Studies is firm.

It is important to bring all documents, forms and supplies with you when you file your thesis or dissertation. Please review the checklist for master's or doctoral students prior to your appointment.

2.1.7 Title Page

Graduate Studies does not supply the title page. You must prepare your title page in accordance with the sample. The title page is to be signed by all members of your committee when they have approved the thesis or dissertation. Only the original title page will be accepted with the thesis or dissertation.

2.1.8 Dissertation Abstracts

Master's theses and doctoral dissertations are required to include an abstract. If your abstract appears in the introductory pages of your thesis/dissertation manuscript, it must follow the same format as the rest of your thesis/dissertation (1 inch margin on all sides, double-spaced, consecutive page numbering, etc.).

A separate abstract is submitted to ProQuest Information and Learning (PQIL) during the electronic submission process and must be formatted following the guidelines on the ETD website. It is important to write an abstract that gives a clear description of the content and major divisions of the thesis/dissertation, since PQIL will publish the abstract exactly as submitted.

Students completing their requirements under doctoral Plan A should provide copies of the abstract for use by the dissertation committee during the examination.

2.1.9 Diploma

When you file your thesis or dissertation, you will receive a Letter of Certification that states you have completed all the requirements for your degree and which will provide the official conferral date of your degree. This certificate may be given to your employer for proof of degree until the Registrar's Office issues an official transcript or diploma. You must complete a form to request your transcript or diploma. Official transcripts normally are available two months after the official degree conferral date, diplomas normally are available four months after this date.

2.1.10 Copyright and Publication

The copyright law of the United States is quite complex. The information contained in this section is only a general guide – more detailed information must be obtained from other sources.

Whether or not you copyright your thesis or dissertation, you retain the right to publish all or any part of it by any means at any time, except for reproduction from a negative microfilm as described in the agreement with PQIL. Should you decide to copyright your thesis or dissertation, you must include a separate unnumbered copyright page after the title page. By adding this copyright notice, which should be included in all copies you distribute, you have copyrighted your thesis or dissertation. At this point you have several options:

You may have the copyright registered for you by PQIL. Along with the UMI Doctoral Dissertation Agreement, you will need to submit a fee to cover the copyright cost.

You may register the copyright yourself by submitting to the Registrar of Copyrights the appropriate application form, a filing fee and one or two copies of the work. In order to have full protection against infringement, this should be done as soon as possible. Information and forms can be obtained from the Registrar of Copyrights, Library of Congress, Washington D.C. 20559.

You may choose to copyright your thesis or dissertation by adding the copyright notice, submitting a copy to the Registrar of Copyrights, but not registering it. (Federal copyright law requires that copies of all works published with notices of copyright be deposited with

the Library of Congress, even if the copyright is not registered). However, to protect your rights in a copyright dispute and in order to be compensated for damages caused by infringement, your copyright must be registered.

2.1.11 Filing Fee

The Filing Fee was established expressly to assist those students who have completed all requirements for degrees except filing theses or dissertations and/or taking final examinations (master's comprehensive exams or doctoral final examinations) and are no longer using University facilities. The Filing Fee is a reduced fee paid in lieu of registration fees. It is assessed only once and must be paid to the Cashier's Office prior to submission of the form to Graduate Studies. Filing Fee status restrictions (more restrictions are noted on the application instruction sheet):

- You may not be using University facilities;
- You cannot be using faculty time other than the time involved in the final reading of the thesis or dissertation or in holding final examinations;
- You are not eligible to hold any academic appointment title for more than 1 quarter;
- You cannot hold a fellowship or receive financial aid.

If you are eligible to use the Filing Fee procedure, you should complete a Filing Fee application, obtain the signature of the Graduate Adviser and your Committee chair, and return the application to Graduate Studies before you stop registering. The Filing Fee must be paid prior to submitting the application to Graduate Studies.

Original (initial) filing fee deadlines adhere to registration deadlines. For example, if you were approved for one quarter of filing fee, you would be eligible to submit your dissertation or thesis up to the last day of late registration for the following quarter. If you do not submit by that date your filing fee status will expire and you would need to secure an extension from your program and from Graduate Studies. Filing fee extensions end the date noted on the petition. Make sure your filing fee is current before you submit your dissertation or thesis.

Chapter 3

Examples of Formatting and Commands

The following chapter shows various formatting and sectioning commands. It also includes examples of how to insert figures and tables into the document. These examples are by no means comprehensive, they are just a sample of what can be done with the power of L^AT_EX.

Filing your dissertation or thesis is the last step in the process leading to the awarding of your degree. The final copy of your thesis or dissertation, which is ultimately deposited in the University Library, becomes a permanent and official record.

3.1 First Section Title – A Particularly Long Section Title with a Special Title for the TOC

A short version of the section title can be included in square brackets just before the full title. This applies to subsections as well.

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Paragraph Title I have no idea who would use sectioning down to the paragraph level in a dissertation, but it is available for those who think it is necessary.

3.2 Some Examples of Figures and Tables

A table such as that shown in Table 3.1 can be included easily. The hard part will be creating the table. Filing your dissertation or thesis is the last step in the process leading to the awarding of your degree. The final copy of your thesis or dissertation, which is ultimately deposited in the University Library, becomes a permanent and official record.

One	Two
Three	Four

Table 3.1. An example of a table. Notice the caption is centered except when it runs longer than a single line on the page.

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One	Two
Three	Four

Table 3.2. Another example of a table.

in the University Library, becomes a permanent and official record.

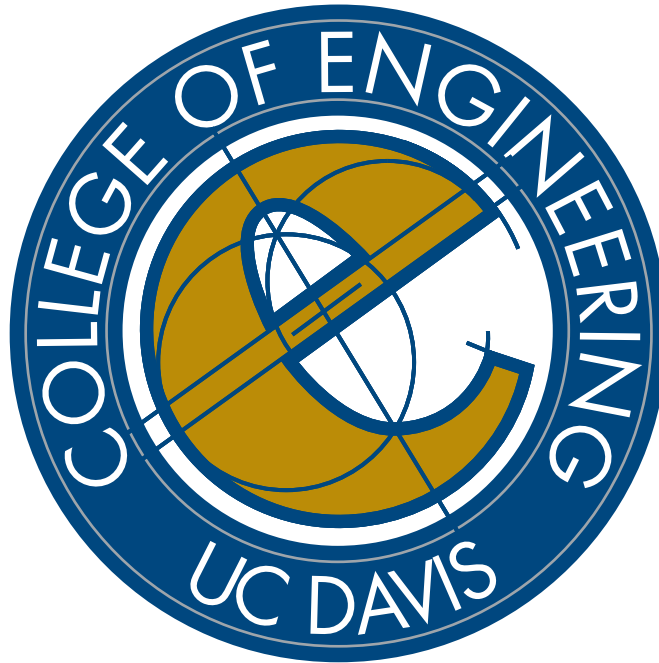


Figure 3.1. A sample figure.

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Figure 3.2. A reduced version of the sample figure.

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