PHYLOGENETIC
COMPARATIVE METHODS

FIONA JORDAN
excd.org
fiona.jordan@bristol.ac.uk
@fiona_jordan

design & diversity

trees are tools
for testing hypotheses

Pagel, M (1997) *Zoologica Scripta*

trees are tools
for testing hypotheses

coupled with data on the characteristics, behaviours, and lifestyles of species, phylogenies can be used to infer the historical evolutionary processes that must have existed in the past, given the patterns of diversity seen in the present. This is a simple but important point because it asserts that the combination of phylogeny and contemporary data are sufficient to infer what the past was like and how it got to be like the present.

Pagel, M (1997) *Zoologica Scripta*

Phylogenetic comparative methods

A suite of computational and statistical tools,
for investigating hypotheses,
about the evolution of a set of traits,
against the background of their evolutionary relationships.

Ord & Martins 2009

Phylogenetic comparative methods

A suite of computational and statistical tools,
for investigating hypotheses,
about the evolution of a set of traits,
against the background of their evolutionary relationships.

Ord & Martins 2009

Phylogenetic comparative methods

A suite of computational and statistical tools,
for investigating hypotheses,
about the evolution of a set of traits,
against the background of their evolutionary relationships.

Let us explain diversity using phylogenetic history.

Originally developed for the study of adaptation by comparing suites of traits across species.

Formalised by Felsenstein (1985) in a classic paper.

Ord & Martins 2009 / Felsenstein 1985

Phylogenies and the comparative method

- **Species** data points might not be independent

Felsenstein 1985

Phylogenies and the comparative method

- **Species** data points might not be independent

Felsenstein 1985

Phylogenies and the comparative method

- **Species** data points might not be independent

Felsenstein 1985

Phylogenies and the comparative method

- **Species** data points might not be independent

Felsenstein 1985

Phylogenies and the comparative method

- **Species** data points might not be independent

Felsenstein 1985

Phylogenies and the comparative method

- **Species** data points might not be independent

Felsenstein 1985

Phylogenies and the comparative method

- **Species** data points might not be independent

Felsenstein 1985

Hierarchical structuring of evolutionary history

Felsenstein 1985

Hierarchical structuring of evolutionary history

- *"Species are part of a hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution."*

Felsenstein 1985

Hierarchical structuring of evolutionary history

- *"Species are part of a hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution."*

- Can't just *sample* taxa because we simply push back the unknown effect of hierarchical structure.

Felsenstein 1985

Hierarchical structuring of evolutionary history

- *"Species are part of a hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution."*

- Can't just *sample* taxa because we simply push back the unknown effect of hierarchical structure.

- This "control for phylogeny" is not just important in studying correlated evolution

  Important in ALL analyses of traits that have an evolutionary history INCLUDING linguistic and cultural features

Felsenstein 1985

Galton's Problem

It was extremely desirable for the sake of those who may wish to study the evidence for Dr. Tylor's conclusions, that full information should be given as to the degree in which the customs of the tribes and races which are compared together are independent. It might be, that some of the tribes had derived them from a common source, so that they were duplicate copies of the same original. Certainly, in such an investigation as this, each of the

Historical relatedness means that traits cannot be assumed to have arisen anew in each population: data points may not be independent of one another.

Galton, in reply to Tylor 1889

Galton's Problem

It was extremely desirable for the sake of those who may wish to study the evidence for Dr. Tylor's conclusions, that full information should be given as to the degree in which the customs of the tribes and races which are compared together are independent. It might be, that some of the tribes had derived them from a common source, so that they were duplicate copies of the same original. Certainly, in such an investigation as this, each of the

to permanent settlement. The difficulty raised by Mr. Galton that some of the concurrences might result from transmission from a common source, so that a single character might be counted several times from its mere duplicates, is a difficulty ever present in such investigations, as for instance in the Malay region, where

Historical relatedness means that traits cannot be assumed to have arisen anew in each population: data points may not be independent of one another.

Galton, in reply to Tylor 1889

Current Anthropology Volume 35, Number 5, December 1994
© 1994 by The Wenner-Gren Foundation for Anthropological Research. All rights reserved 0011-3204/94/3505-0001$2.50

The Comparative Method in Anthropology[1]

by Ruth Mace
and Mark Pagel

Cross-cultural comparison is a common method of testing hypotheses regarding the co-evolution of elements of cultures or of the adaptiveness of a cultural practice to some aspect of the environment. It has long been recognized, however, that cultures are not independent but rather may share many cultural elements by virtue of common ancestry and proximity. Attempts to address this issue, known as Galton's problem, range from statistically removing confounding variables to using a standard sample of "independent cultures." We show here that when testing any hypothesis of co-evolution one should not attempt to identify independent cultures or to create them statistically. Rather, cross-cultural comparative studies must be based upon the identification of independent events of cultural change. Once this principle is applied, it becomes apparent that it is in fact groups of closely related cultures that are potentially the most informative for testing cross-cultural hypotheses. Constructing phylogenies of cultures and placing upon them independent instances of cultural elements' arising or changing is an essential part of this task.

Ruth Mace is a Royal Society University Research Fellow in the Department of Anthropology of University College London (Gower St., London WC1E 6BT, England). Born in 1961, she was educated at Oxford University (B.A., 1983; D.Phil., 1987) and has held research positions in the Centre for Environmental Technology of Imperial College (1987–89) and the School of Development Studies of the University of East Anglia (1989–91). Her research interests are subsistence economics, pastoralism, human ecology, and conservation. She has published "Pastoralist Strategies for Survival in an Unpredictable Environment: A Model of Herd Composition" (*Agricultural Systems* 31:185–204), "Overgrazing Overstated" (*Nature* 349:280–91), "Nomadic Pastoralists Adopt Strategies That Maximise Long-term Household Survival" (*Behavioural Ecology and Sociobiology* 33:329–34), and "Transitions between Cultivation and Pastoralism in Sub-Saharan Africa" (CA 34:363–82).

Mark Pagel directs a research unit on ecology and behaviour in the Department of Zoology of Oxford University. He was born in 1954 and educated at the University of Washington (B.A., 1976; Ph.D., 1980). He has taught evolutionary theory and statistics at Harvard University (1990–92) as well as at Oxford. His publications include "Detecting Correlated Evolution on Phylogenies: A General Method for the Comparative Analysis of Discrete Characters" (*Proceedings of the Royal Society* B 255:37–45), "The Adaptationist Wager," in *Phylogenetics and Ecology*, edited by P. Eggleton and D. Vane-Wright (London: Academic Press, in press), "The Evolution of Conspicuous Oestrous Advertisement in Old World Monkeys" (*Animal Behaviour* 47:1333–41), and, with P. H. Harvey, *The Comparative Method in Evolutionary Biology* (Oxford: Oxford University Press, 1991).

1. This research was funded by the Royal Society (RM) the Science and Engineering Research Council, the National Environment Research Council, and the Biotechnology and Biological Sciences Research Council (MP).

The present paper was submitted in final form 6 xii 93.

For well over a century, anthropologists have used information obtained by comparisons across cultures to test ideas about cultural evolution. Since the 1950s many of these comparisons have made use of tabulations of cultural information compiled by G. P. Murdock and others, who codified over 1,250 cultures extant at that time. Shortly after the first studies making use of Murdock's *Atlas of World Cultures* were published, a large branch of anthropology (mostly located in Britain) reacted to the use of facts about culture in this way. The idea that the facts themselves should be considered as social constructs came into the ascendancy, and much of anthropology redefined itself as an interpretive humanity rather than a science, concerned with cultural specificity rather than comparison across cultures. Holý (1987) remarked that "the line between comparativists and non-comparativists is probably more sharply drawn than ever before," the latter being in the numerical majority.

Meanwhile, the past decade has seen a great expansion in other branches of anthropology in which anthropologists study humanity, including cultural diversity, as a scientific endeavour. Here the comparative method is widely used both by those who are interested in the evolution of culture and in other disciplines of the human sciences, such as demography, in which, for example, fertility is considered to be at least in part cultural. Issues that have recently been addressed using cross-cultural comparison as empirical evidence include questions concerning the co-evolution of rules of inheritance and marriage (Hartung 1982, 1985), pathogen risk and polygyny (Low 1988, 1990), incest taboos and exogamy (Durham 1991, Thornhill 1991), reproduction and social organization (Lesthaeghe 1989), and modes of subsistence and fertility (Campbell and Wood 1988, Bentley, Goldberg, and Jasienska 1993).

Most models of cultural evolution include the assumption that culture evolves by "descent with modification" (Cavalli-Sforza and Feldman 1981, Lumsden and Wilson 1981, Boyd and Richerson 1985, Durham 1991), probably from a single origin. Most models of cultural evolution also acknowledge the existence of bundles of characters that can be transmitted as independent units (i.e., even when other aspects of the culture are not passed on); we shall call these "elements" of culture.

Perhaps the most common way of analysing comparative data is to correlate two or more elements across a group of cultures. However, Francis Galton realized as early as 1889 that cultures cannot be treated as independent for purposes of investigating cross-cultural trends.

Mace & Pagel 1994

Current Anthropology Volume 35, Number 5, December 1994
© 1994 by The Wenner-Gren Foundation for Anthropological Research. All rights reserved 0011-3204/94/3505-0001$2.50

The Comparative Method in Anthropology[1]

by Ruth Mace
and Mark Pagel

Cross-cultural comparison is a c
hypotheses regarding the co-evol
of the adaptiveness of a cultural
environment. It has long been re
are not independent but rather n
ments by virtue of common anc
address this issue, known as Gal
tically removing confounding va
ple of "independent cultures." W
any hypothesis of co-evolution o
tify independent cultures or to c
cross-cultural comparative studi
fication of independent events o
ciple is applied, it becomes appa
closely related cultures that are
for testing cross-cultural hypoth
of cultures and placing upon the
tural elements' arising or changi
task.

RUTH MACE is a Royal Society
the Department of Anthropology
(Gower St., London WC1E 6BT, England). Born in 1961, she was educated at Oxford University (B.A., 1983; D.Phil., 1987) and has held research positions in the Centre for Environmental Technology of Imperial College (1987–89) and the School of Development Studies of the University of East Anglia (1989–91). Her research interests are subsistence economics, pastoralism, human ecology, and conservation. She has published "Pastoralist Strategies for Survival in an Unpredictable Environment: A Model of Herd Composition" (*Agricultural Systems* 31:185–204), "Overgrazing Overstated" (*Nature* 349:280–91), "Nomadic Pastoralists Adopt Strategies That Maximise Long-term Household Survival" (*Behavioural Ecology and Sociobiology* 33:329–34), and "Transitions between Cultivation and Pastoralism in Sub-Saharan Africa" (CA 34:363–82).

MARK PAGEL directs a research unit on ecology and behaviour in the Department of Zoology of Oxford University. He was born in 1954 and educated at the University of Washington (B.A., 1976; Ph.D., 1980). He has taught evolutionary theory and statistics at Harvard University (1990–92) as well as at Oxford. His publications include "Detecting Correlated Evolution on Phylogenies: A General Method for the Comparative Analysis of Discrete Characters" (*Proceedings of the Royal Society* B 255:37–45), "The Adaptationist Wager," in *Phylogenetics and Ecology*, edited by P. Eggleton and D. Vane-Wright (London: Academic Press, in press), "The Evolution of Conspicuous Oestrous Advertisement in Old World Monkeys" (*Animal Behaviour* 47:1333–41), and, with P. H. Harvey, *The Comparative Method in Evolutionary Biology* (Oxford: Oxford University Press, 1991).

The present paper was submitted in final form 6 XII 93.

For well over a century, anthropologists have used infor-

The critical point of this essay is that the validity of comparative methods for anthropology depends upon correctly counting independent instances of cultural change. Independent instances of cultural change, in turn, cannot be identified without the construction of a phylogeny (or cladogram) showing the patterns of hierarchical descent of the cultures being studied.

issues that have recently been addressed using cross-cultural comparison as empirical evidence include questions concerning the co-evolution of rules of inheritance and marriage (Hartung 1982, 1985), pathogen risk and polygyny (Low 1988, 1990), incest taboos and exogamy (Durham 1991, Thornhill 1991), reproduction and social organization (Lesthaeghe 1989), and modes of subsistence and fertility (Campbell and Wood 1988, Bentley, Goldberg, and Jasienska 1993).

Most models of cultural evolution include the assumption that culture evolves by "descent with modification" (Cavalli-Sforza and Feldman 1981, Lumsden and Wilson 1981, Boyd and Richerson 1985, Durham 1991), probably from a single origin. Most models of cultural evolution also acknowledge the existence of bundles of characters that can be transmitted as independent units (i.e., even when other aspects of the culture are not passed on); we shall call these "elements" of culture.

Perhaps the most common way of analysing comparative data is to correlate two or more elements across a group of cultures. However, Francis Galton realized as early as 1889 that cultures cannot be treated as independent for purposes of investigating cross-cultural trends.

1. This research was funded by the Royal Society (RM) the Science and Engineering Research Council, the National Environment Research Council, and the Biotechnology and Biological Sciences Research Council (MP).

Mace & Pagel 1994

“the largest and most important aspects of culture leave no trace in the soil; language, social organization, religion - in short, everything that is not material - vanishes with the life of each generation.”

Franz Boas 1948

“the largest and most important aspects of culture leave no trace in the soil; language, social organization, religion - in short, everything that is not material - vanishes with the life of each generation.”

Franz Boas 1948

Comparative methods for all seasons

- All have in common that we're examining the evolution of characters on trees, *not* building trees with those characters.

data exploration	inferring models of evolution
inferring ancestral states	phylogenetic signal
correlated evolution	transmission
tempo and mode	biocultural coevolution

Gray et al 2007 / Jordan 2011 / Nunn 2011

Fertility and Mode of Subsistence: A Phylogenetic Analysis[1]

DANIEL W. SELLEN AND RUTH MACE
Department of Anthropology, University College London, Gower St., London WC1E 6BT, U.K. 3 III 97

Evolved structure of language shows lineage-specific trends in word-order universals

Michael Dunn[1,2], Simon J. Greenhill[3,4], Stephen C. Levinson[1,2] & Russell D. Gray[3]

A Phylogenetic Analysis of the Evolution of Austronesian Sibling Terminologies

FIONA M. JORDAN[1]

From Bridewealth to Dowry?

A Bayesian Estimation of Ancestral States of Marriage Transfers in Indo-European Groups

Laura Fortunato, Clare Holden, and Ruth Mace
University College London

Testing for Divergent Transmission Histories among Cultural Characters: A Study Using Bayesian Phylogenetic Methods and Iranian Tribal Textile Data

Luke J. Matthews[1]*, Jamie J. Tehrani[2], Fiona M. Jordan[3], Mark Collard[4,5], Charles L. Nunn[1]

Evolutionary History of Hunter-Gatherer Marriage Practices

Robert S. Walker[1]*, Kim R. Hill[2], Mark V. Flinn[1], Ryan M. Ellsworth[1]

Matrilocal residence is ancestral in Austronesian societies

Fiona M. Jordan[1,2,*], Russell D. Gray[3], Simon J. Greenhill[3] and Ruth Mace[1,2]

Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis

Clare Janaki Holden* and Ruth Mace

THE EVOLUTION OF HUMAN SEX RATIO AT BIRTH: A BIO-CULTURAL ANALYSIS

Ruth Mace and Fiona Jordan

Rise and fall of political complexity in island South-East Asia and the Pacific

Thomas E. Currie[1,2], Simon J. Greenhill[3,4], Russell D. Gray[3], Toshikazu Hasegawa[1] & Ruth Mace[2]

Models of change for discrete data

Components of a comparative analysis

Components of a comparative analysis

data

model

inference method

parameter estimates

trees

tip data

Components of a comparative analysis

Components of a comparative analysis

Components of a comparative analysis

data	model	inference method	parameter estimates
trees tip data	change description	MP ML Bayesian	node values transition rates

Modelling change on phylogenies

Ord & Martins 2010 / Nunn 2011

Modelling change on phylogenies

- Discrete and continuous characters change differently

  Different model/assumptions required

Ord & Martins 2010 / Nunn 2011

Modelling change on phylogenies

- Discrete and continuous characters change differently

  Different model/assumptions required

- Same types of inference methods as for tree-building

  Parsimony
  Maximum likelihood
  Bayesian

  ... and the same pros and cons.

Ord & Martins 2010 / Nunn 2011

Modelling change on phylogenies

- Discrete and continuous characters change differently

  Different model/assumptions required

- Same types of inference methods as for tree-building

  Parsimony

  Maximum likelihood

  Bayesian

  ... and the same pros and cons.

- PCMs implemented in a wide range of software packages

  Mesquite, BayesTraits, R, Compare, Brownie

Ord & Martins 2010 / Nunn 2011

Discrete data in a probabilistic framework

Pagel 1994

Discrete data in a probabilistic framework

state at end of branch

state at
beginning
of branch

Pagel 1994

Discrete data in a probabilistic framework

state at end of branch

	0	1

state at beginning of branch

Pagel 1994

Discrete data in a probabilistic framework

state at end of branch

	0	1

state at beginning of branch

Pagel 1994

Discrete data in a probabilistic framework

state at end of branch

state at beginning of branch	0	1
0	$q00$	$q01$

Pagel 1994

Discrete data in a probabilistic framework

state at end of branch

	0	1
0	$q00$	$q01$

state at beginning of branch

Pagel 1994

Discrete data in a probabilistic framework

state at end of branch

	0	1
0	$q00$	$q01$

state at beginning of branch

Pagel 1994

Discrete data in a probabilistic framework

state at end of branch

state at beginning of branch	0	1
0	$q00$	$q01$
1	$q10$	$q11$

Pagel 1994

Discrete data in a probabilistic framework

continuous-time Markov models

these specify a matrix [Q] of transition probabilities

probability of change at each tiny increment along branch

Pagel 1994

transition-rate parameters

describe the probability of change from one state to another

Pagel 1999 *Systematic Biology* / Pagel & Meade 2004 *American Naturalist*

Modelling discrete change on phylogenies

- The TREES are treated as fixed, like the DATA
- Very similar to estimating the evolution of a single character when inferring phylogenies
- More fine-grained investigation of the model of evolution.

Ancestral state inference

Specifying and testing a model of discrete character evolution

Components of a comparative analysis

Components of a comparative analysis

data

model

inference method

parameter estimates

trees

tip data

Components of a comparative analysis

Components of a comparative analysis

Components of a comparative analysis

data	model	inference method	parameter estimates
trees tip data	change description	MP ML Bayesian	***node values*** transition rates

Phylogeny
affects our estimates of ancestral states

Ancestral states
What kinds of questions?

- What is the earlier form of a trait?
- What form of the trait do we see at a specific node?
- How certain are we in our estimates of node values?
- Given some independent evidence about ancestral forms, how much do we prefer one hypothesis over another?
- Does altering the ancestral states affect our model of evolution?
  If so, for better or worse?

Loss and recovery of wings in stick insects

Michael F. Whiting*, Sven Bradler† & Taylor Maxwell‡

Whiting *et al* 2003 *Nature*

Loss and recovery of wings in stick insects

Michael F. Whiting*, Sven Bradler† & Taylor Maxwell‡

- Winged
- Wingless

- *Oligotoma nigra*
- *Teratembia n.* sp.
- *Timema knulii*
- *Oreophoetes peruana*
- *Libethra regularis*
- *Diapheromera* sp.
- *Diapheromera femorata*
- *Baculum thaii*
- *Gratidia fritzschei*
- *Sceptrophasma hispidula*
- *S. langikawicensis*
- *Baculini* spec. indet.
- *Medauroidea extradentatum*
- *Medaura* sp.
- *Oncotophasma martini*
- *Bacillius rossius*
- *Carausius morosus*
- *Eurycantha insularis*
- *Phyllium bioculatum*
- *Neohirasea maerens*
- *Neohirasea* sp.
- *Sipyloidea sipylus*
- *Pseudodiacantha macklottii*
- *Lopaphus perakensis*
- *Lopaphus sphalerus*
- *Phobaeticus heusii*
- *Lamponius guerini*
- *Dimorphodes prostasis*
- *Tropiderus childrenii*
- *Eurycnema goliath*
- *Ctenomorphodes briareus*
- *Extatosoma tiaratum*
- *Anisomorpha ferruginea*
- *Pseudophasma rufipes*
- *Aretaon asperrimus*
- *Sungaya inexpectata*
- *Agathemera crassa*
- *Heteropteryx dilatata*
- *Haaniella dehaanii*

Loss and recovery of wings in stick insects

Michael F. Whiting*, Sven Bradler† & Taylor Maxwell‡

Ancestral states are always *estimates* (ASE)

1. posterior distribution of trees to account for “phylogenetic uncertainty”

Ancestral states are always *estimates* (ASE)

1. posterior distribution of trees to account for “phylogenetic uncertainty”

Ancestral states are always *estimates* (ASE)

1. posterior distribution of trees to account for “phylogenetic uncertainty”

Ancestral states are always *estimates* (ASE)

1. posterior distribution of trees to account for “phylogenetic uncertainty”

2. map trait data onto tree at tips

Ancestral states are always *estimates* (ASE)

1. posterior distribution of trees to account for “phylogenetic uncertainty”

2. map trait data onto tree at tips

3. estimate ancestral state at nodes to get “character uncertainty”: represented by probability of each ancestral state

Ancestral states are always *estimates* (ASE)

1. posterior distribution of trees to account for “phylogenetic uncertainty”

2. map trait data onto tree at tips

3. estimate ancestral state at nodes to get “character uncertainty”: represented by probability of each ancestral state

Ancestral states are always *estimates* (ASE)

1. posterior distribution of trees to account for "phylogenetic uncertainty"

2. map trait data onto tree at tips

3. estimate ancestral state at nodes to get "character uncertainty": represented by probability of each ancestral state

4. condition each ASE on that node's posterior probability on the tree. e.g. the arrowed node has pr(●) = .5 × .9 = .45

Steps
in ancestral state inference

Steps
in ancestral state inference

- REQUIREMENTS: Trait data, tree(s), question, method

Steps
in ancestral state inference

- REQUIREMENTS: Trait data, tree(s), question, method

- IMPLEMENTATION: Mesquite, BayesTraits, APE, geiger … [R]

Steps
in ancestral state inference

- REQUIREMENTS: Trait data, tree(s), question, method

- IMPLEMENTATION: Mesquite, BayesTraits, APE, geiger … [R]

- Designate which nodes are to be inferred: (root? all? some?)
  - Incorporate any independent evidence on prehistory using a “fossilisation” procedure to fix a state at a node.
  - Incorporate any independent evidence on process (different models of change)

Steps
in ancestral state inference

- REQUIREMENTS: Trait data, tree(s), question, method

- IMPLEMENTATION: Mesquite, BayesTraits, APE, geiger … [R]

- Designate which nodes are to be inferred: (root? all? some?)
  - Incorporate any independent evidence on prehistory using a "fossilisation" procedure to fix a state at a node.
  - Incorporate any independent evidence on process (different models of change)

- Examine the distributions of obtained node values

Steps
in ancestral state inference

- REQUIREMENTS: Trait data, tree(s), question, method

- IMPLEMENTATION: Mesquite, BayesTraits, APE, geiger … [R]

- Designate which nodes are to be inferred: (root? all? some?)
  - Incorporate any independent evidence on prehistory using a "fossilisation" procedure to fix a state at a node.
  - Incorporate any independent evidence on process (different models of change)

- Examine the distributions of obtained node values

- Test how robust the ASE is under different models of evolution using LRT / BF tests

Let’s do the time warp …

postmarital residence

matrilocal

patrilocal

neolocal

Inferring ancestral residence
What did we do?

Jordan *et al* 2009 *Proceedings B*

Inferring ancestral residence
What did we do?

- Used independently-derived lexical phylogenies of AN languages
  - Matched ethnographic descriptions to linguistic groups

Jordan *et al* 2009 *Proceedings B*

Inferring ancestral residence
What did we do?

- Used independently-derived lexical phylogenies of AN languages

  Matched ethnographic descriptions to linguistic groups

- Data on residence was coded as ONE TRAIT with TWO STATES

  Societies could have mixed strategies e.g. MP = ambilocal

Jordan *et al* 2009 *Proceedings B*

Inferring ancestral residence
What did we do?

- Used independently-derived lexical phylogenies of AN languages
  Matched ethnographic descriptions to linguistic groups

- Data on residence was coded as ONE TRAIT with TWO STATES
  Societies could have mixed strategies e.g. MP = ambilocal

- Used Multistate in BayesTraits to infer ancestral states and the parameters of the most likely model of evolution
  Tested our hypotheses over a posterior sample of 1000 trees
  Used reversible-jump MCMC procedure to help find the best model of evolution
  "Fossilised" early nodes to each possible state to test for early matrilocal

Jordan *et al* 2009 *Proceedings B*

Inferring ancestral residence
What did we do?

- Used independently-derived lexical phylogenies of AN languages
  Matched ethnographic descriptions to linguistic groups

- Data on residence was coded as ONE TRAIT with TWO STATES
  Societies could have mixed strategies e.g. MP = ambilocal

- Used Multistate in BayesTraits to infer ancestral states and the parameters of the most likely model of evolution
  Tested our hypotheses over a posterior sample of 1000 trees
  Used reversible-jump MCMC procedure to help find the best model of evolution
  "Fossilised" early nodes to each possible state to test for early matrilocal

- Compared the Lh of each "version of history" using the BF test

Jordan *et al* 2009 *Proceedings B*

Jordan et al 2009 *Proceedings B*

maori
hawaiian
tahitian
tongarevan
mangaian
tuamotu
marquesan
mangarevan
rapanui
tuvalu
tokelau
kapinga
ontong java
tikopia a
rennellese
niue
eastuvea
eastfutuna
tongan
samoan
rotuman
fijian
chuuk
woleaian
carolinian
nomoian
marshallese
ponape
kusaie
kiribati
simbo
roviana
choiseul
nissan
koobe
ulawan
kwaio
kaoka
nguna
mota
eromanga
lifu
nelemwa
santacruz
aua
manus
dobuan
molima
bwaidoga
dahuni
trobriand
mekeo
motu
manam
wogeo
sengseng
lakalai
giman
buli
misool
numfor
waropen
babar
letinese
erai
kisar
roti
atoni
belu
tanimbarese
irarutu
kei
ambon
ilimandiri
kedang
sika
manggarai
kodi
sumbanese
sumbawanese
palauan
chamorro
nias
mori
ponerate
banggai
bugiinese
toradja
macassarese
kerinci
minangkabau
ogan
melayu
iban
sundanese
madurese
javanese
gayo
fobabatak
bali
moken
cham
punan
modang
kenyah
melanau
ngajudayak
malagasy
dusun
tagbanua
palawanbatak
hanunoo
sugbuhanon
bisayan
subanun
manobo
bilaan
maranao
bontok
sagadaigorot
ifugao
kalinga
ilongot
gaddang
agta
yami
bolaang
bajau
paiwan
puyuma
buhun
ami
tsou
saisiat
atayal

Jordan et al 2009 *Proceedings B*

Matrilocal residence is ancestral in Austronesian societies

Fiona M. Jordan[1,2,*], Russell D. Gray[3], Simon J. Greenhill[3] and Ruth Mace[1,2]

Jordan et al 2009 *Proceedings B*

Inferring ancestral residence
What did we do?

Jordan *et al* 2009 *Proceedings B*

Inferring ancestral residence
What did we do?

- We inferred a node's state by multiplying:
  - our character certainty about the state (e.g. .95 patrilocal)
  - our phylogenetic certainty that the node existed i.e. the posterior probability

Jordan *et al* 2009 *Proceedings B*

Inferring ancestral residence
What did we do?

- We inferred a node's state by multiplying:
  - our character certainty about the state (e.g. .95 patrilocal)
  - our phylogenetic certainty that the node existed i.e. the posterior probability

- We used "fossilisation" procedures to test the robustness of our inferences about residence.

- We compared one- and two- parameter models and found evidence for unequal rates of change.

Jordan *et al* 2009 *Proceedings B*

Inferring ancestral residence
What did we do?

- We inferred a node's state by multiplying:
  - our character certainty about the state (e.g. .95 patrilocal)
  - our phylogenetic certainty that the node existed i.e. the posterior probability

Table 1. Comparing model support with the Bayes factor. (Bayes factors were calculated as follows: BF = 2(ln LhA − ln LhB), where ln Lh*x* is the marginal likelihood (i.e. the harmonic mean of the post-convergence ln likelihoods, allowing us to compare the posterior distributions). BF values indicate evidence in favour of model A: 0–2, barely worth mentioning; 2–6, positive; 6–10, strong; above 10, very strong/decisive (Kass & Raftery 1995). Negative values favour model B. m, matrilocal; p, patrilocal.)

model A	ln Lh	model B	ln Lh	BF	verbal description
PAN-m	−61.36	PAN-p	−62.49	2.26	positive evidence for matrilocality
PMP-m	−60.80	PMP-p	−64.99	8.38	strong evidence for matrilocality
POC-m	−62.79	POC-p	−61.50	−2.58	positive evidence for patrilocality
equal rates	−63.12	default	−59.61	−7.03	strong evidence for unequal rates of character change

PCEMP

- We compared one- and two- parameter models and found evidence for unequal rates of change.

Jordan *et al* 2009 *Proceedings B*

Modelling evolutionary change

Modelling change
What kinds of questions?

Modelling change
What kinds of questions?

- How do traits change their state?

Modelling change
What kinds of questions?

- How do traits change their state?
- Do traits change sequentially/stepwise, or are all changes possible?

Modelling change
What kinds of questions?

- How do traits change their state?
- Do traits change sequentially/stepwise, or are all changes possible?
- Are some types of changes more likely than others?

Modelling change
What kinds of questions?

- How do traits change their state?
- Do traits change sequentially/stepwise, or are all changes possible?
- Are some types of changes more likely than others?
- Do gains and losses happen at equal rates?

Modelling change
What kinds of questions?

- How do traits change their state?
- Do traits change sequentially/stepwise, or are all changes possible?
- Are some types of changes more likely than others?
- Do gains and losses happen at equal rates?
- Which model of change is preferred when we compare hypotheses?

Modelling change
What kinds of questions?

- How do traits change their state?
- Do traits change sequentially/stepwise, or are all changes possible?
- Are some types of changes more likely than others?
- Do gains and losses happen at equal rates?
- Which model of change is preferred when we compare hypotheses?
- How do models of change compare across different groups of taxa?

Steps
in modelling evolutionary change

- REQUIREMENTS: Trait data, tree(s), question, method

- IMPLEMENTATION: Mesquite, BayesTraits, R packages

- PROCESS:
  First infer an unrestricted model of evolution
  Specify any restrictions or conditions
  Compare models using LRT or Bayes Factors
  ... Compare dynamics across groups of taxa (e.g. language families)

data on traits
across populations

data on traits
across populations

language phylogenies
as population history

data on traits
across populations

language phylogenies
as population history

a model of
how traits evolve
(and ancestral states)

data on traits
across populations

language phylogenies
as population history

a model of
how traits evolve
(and ancestral states)

data on traits
across populations

language phylogenies
as population history

a model of
how traits evolve
(and ancestral states)

data on traits
across populations

language phylogenies
as population history

a model of
how traits evolve
(and ancestral states)

actual data

simulate evolution from all possible starting states

actual data

simulate evolution from all possible starting states

actual data

simulation one

actual data

simulation one

actual data

simulation one

actual data

simulation one

actual data

simulation one

actual data

simulation one

actual data

simulation one

actual data
simulation one

actual data
simulation one

actual data
simulation one

actual data
simulation one

actual data

simulated data

simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

actual data
simulated data
simulation one

simulation one

simulation one

actual data
simulated data
3
2
model likelihood score
simulation one

actual data

simulate evolution from all possible starting states

actual data

simulate evolution from all possible starting states

actual data

simulation two

actual data

simulation two

actual data

simulation two

actual data

simulation two

actual data

simulation two

actual data

simulation two

actual data

simulation two

actual data

simulation two

actual data
simulation two

actual data

simulated data

simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

actual data
simulated data
simulation two

simulation two

simulation two

actual data
simulated data
3
1
model likelihood score
simulation two

we combine KNOWN data & phylogenies
and INFER the best models & ancestral states

How do characters evolve?

- ORDERED CHANGE
  Sequential model

How do characters evolve?

- UNORDERED CHANGE
  all changes are possible

How do characters evolve?

- RESTRICTED CHANGE
  some changes are possible, and/or
  some changes are weighted

How do characters evolve?

- RESTRICTED CHANGE
  some changes are possible, and/or
  some changes are weighted

Geoff Kushnick @ ANU
Russell Gray @ MPI-SHH

LAND TENURE

Geoff Kushnick @ ANU
Russell Gray @ MPI-SHH

LAND TENURE

Are there generalised trajectories of cultural change?
If so, what is the pattern of land tenure evolution?

Geoff Kushnick @ ANU
Russell Gray @ MPI-SHH

LAND TENURE

Are there generalised trajectories of cultural change?
If so, what is the pattern of land tenure evolution?

What can we infer about ancestral landownership in Austronesian societies?

Geoff Kushnick @ ANU
Russell Gray @ MPI-SHH

LAND TENURE

Are there generalised trajectories of cultural change?
If so, what is the pattern of land tenure evolution?

What can we infer about ancestral landownership in Austronesian societies?

Which norms have historical signal?

Geoff Kushnick @ ANU
Russell Gray @ MPI-SHH

Nomadic
(no ownership)
Pastoral
(group held land)
Agricultural
(patrilineal kin group ownership)
(individual ownership)
N
None
G
Group
K
Kin
I
Individual
Commons
(common property)
Reciprocal Access
(communal property)
Territoriality
(local group ownership)
Private Property
(kin group ownership)
(individual ownership)

(a)
20
0
−20
100
120
140
160
180
200
−20
50
−40
170
−30
250

Nomadic
(no ownership)
Pastoral
(group held land)
Agricultural
(patrilineal kin group ownership)
(individual ownership)
N
None
G
Group
K
Kin
I
Individual
Commons
(common property)
Reciprocal Access
(communal property)
Territoriality
(local group ownership)
Private Property
(kin group ownership)
(individual ownership)

(a)
Main form of land tenure
no ownership
group ownership
kin-group ownership
individual ownership
Nomadic (no ownership)
Pastoral (group held land)
Agricultural (patrilineal kin group ownership)
(individual ownership)
N None
G Group
K Kin
I Individual
Commons (common property)
Reciprocal Access (communal property)
Territoriality (local group ownership)
Private Property (kin group ownership)
(individual ownership)
(b)
POc
PMP
PAN
Maori
Tahitian
Tongareva
Mangaian
Rapanui
Tuvalu
Tokelau
Kapingamarangi
OntongJava
Tikopia
Futuna
Rennellese
Niuean
EastFutuna
Anuta
Tongan
Samoan
Rotuman
Bau
Truk
Woleaian
Kosrae
Pohnpeian
Kiribati
Tanna
Nguna
Choiseul
NehanHape
Manus
Motu
Mekeo
Dobu
Kilivila
Manam
Kilenge
Sengseng
Lakalai
Rotinese
Atoni
Tetum
Selaru
Kei
Kedang
Lamaholot
Sika
Manggarai
Birma
Banggai
Bonerate
Sangir
Bugis
Toraja
Makassar
Minangkabau
Kerinci
Ogan
Ambonese
Iban
Sunda
Madurese
Javanese
Rejang
Gayo
Abung
TobaBatak
Sasak
Balinese
Moken
Melenau
Penan
Idaan
Mansaka
Tausug
Bisaya
PalawanBatak
Tagbanwa
Hanunoo
Subanun
UplandBagobo
Maranao
Bontok
LepantoSegada
Kalingas
Ilongot
Ibaloi
Gaddang
Agta
Yami
Gorontalo
BolaangMongondow
Yakan
Bajau
Puyuma
Bunun
Ami
Tsou
Atayal

(a)
"Exclusivity Gain"
"Alternative"
Rectilinear
Unilinear
Relaxed Unilinear
Full
No Loss
Loss for Change
Gain from None
Main form of Land Tenure
no ownership
group ownership
kin-group ownership
individual ownership
Unstable Group
Kin-Group
Corporate
N
G
K
I

(b)
none
individual
group
kin
1.0
2.0
0.5
1.0
0.0
0.5
Key to histograms
frequency over 1000 trees
value of rate parameter

(a)
"Exclusivity Gain"
Rectilinear
Unilinear
Relaxed Unilinear
Full
No Loss
Loss for Cha
Unstable Group
Kin-Group
Main form of Land Tenure
no ownership
group ownership
kin-group ownership
individual ownership
(b)
none
individual
group
kin
Key to histograms
frequency over 1000 trees
value of rate parameter
alternative unilinear
alternative relaxed unilinear
loss for change
exclusivity relaxed unilinear
full
gain from none
group unstable
exclusivity unilinear
alternative unlinear equal
kin stable
alternative rectilinear
corporate stable
exclusivity rectilinear
no loss
ΔAICc
1.63
3.56
6.60
7.72
9.08
9.91
10.59
14.61
17.93
26.81
31.66
65.47
89.73
240
250
260
270
300
340
AICc scores

Table 1
Phylogenetic signal of each of the main type of land tenure norms (n = 97).

Land Tenure	D-Statistic[1]		Phylogenetic Signal?
	Median[2]	Range	
None	0.30	−0.09–0.64	Moderate
Individual	1.19***	0.98–1.34	Significant absence
Group	0.87*	0.62–1.09	Significant absence
Kin-Group	0.17***	−0.04–0.29	Significant and strong

[1] D and *p*-values estimated from all 1,000 trees in the posterior.
[2] * 95% $p < 0.05$; *** all $p < 0.005$.

Rise and fall of political complexity in island South-East Asia and the Pacific

Thomas E. Currie[1,2], Simon J. Greenhill[3,4], Russell D. Gray[3], Toshikazu Hasegawa[1] & Ruth Mace[2]

Currie et al. 2010 *Nature*

Type of society	n	description
Acephalous	35	Small independent local communities (i.e. villages), no official positions of political leadership
Simple Chiefdom	28	Official political leader (chief) ruling over a collection of villages
Complex Chiefdom	16	Two levels of political leadership beyond the local community (often other official positions e.g. high priest)
State	5	Three or more supra-local decision-making levels, many political and bureaucratic offices

Evolution of political complexity
What did they do?

Currie *et al* 2010 *Nature*

Evolution of political complexity
What did they do?

- Data on political complexity coded as ONE trait with FOUR states

  Defined their hypotheses as models where traits could change between:

Currie *et al* 2010 *Nature*

Evolution of political complexity
What did they do?

- Data on political complexity coded as ONE trait with FOUR states

  Defined their hypotheses as models where traits could change between:

- Used Multistate in BayesTraits to infer the parameters of the most likely model of evolution (and ASE)

  Tested hypotheses over a posterior sample of 1000 trees

  Used reversible-jump MCMC procedure to help find the best model of evolution

- Compared sequential models to assess which was best supported

Currie *et al* 2010 *Nature*

Evolution of political complexity

Ancestral state estimates

Currie et al. 2010 *Nature*

Evolution of political complexity
Model testing

Figure 2 | Models of political evolution tested in this study. The three models on the white background (UNI, unilinear; RU, relaxed unilinear; REC, rectilinear) represent the idea that political evolution follows a sequence of incremental steps in the direction of increasing complexity, but differ as to whether and how decreases can occur. The three models on the grey background (AT, alternative trajectories; ATR, alternative trajectories (reversible); FULL) allow non-sequential increases in political complexity. Forms of political organization: A, acephalous society; sC, simple chiefdom; cC, complex chiefdom; S, state.

Currie et al. 2010 *Nature*

Currie et al. 2010 *Nature*

Currie et al. 2010 *Nature*

Evolution of political complexity
What did they conclude?

Currie et al. 2010 *Nature*

Evolution of political complexity
What did they conclude?

- A “unilinear” model of stepwise change was the best supported, but a “rectilinear” model was also well-supported.
  In these societies, political complexity only accrues stepwise, but then can “collapse” to less complex forms.

Currie et al. 2010 *Nature*

Evolution of political complexity
What did they conclude?

- A "unilinear" model of stepwise change was the best supported, but a "rectilinear" model was also well-supported.
  In these societies, political complexity only accrues stepwise, but then can "collapse" to less complex forms.

- *"This potential distinction between the patterns of change for increasing and decreasing complexity may be due to it being easier to break up forms of political organization than to develop practices and institutions that enable units to be joined together in a stable manner"*

Currie et al. 2010 *Nature*

Your place or mine? A phylogenetic comparative analysis of marital residence in Indo-European and Austronesian societies

Laura Fortunato[1,2,*,†] and Fiona Jordan[1,2,‡]

Fortunato & Jordan 2010 *Phil Trans Roy Soc London*

The evolution of marital residence

What did we do?

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

The evolution of marital residence
What did we do?

- Used independently-derived lexical phylogenies of AN and IE
  - Matched ethnographic descriptions to linguistic groups

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

The evolution of marital residence
What did we do?

- Used independently-derived lexical phylogenies of AN and IE

  Matched ethnographic descriptions to linguistic groups

- Data on residence was coded as ONE TRAIT with THREE STATES

  Matrilocal, patrilocal, neolocal

  We allowed for mixed strategies e.g. MP = ambilocal and main/alternative forms

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

The evolution of marital residence
What did we do?

- Used independently-derived lexical phylogenies of AN and IE
  Matched ethnographic descriptions to linguistic groups

- Data on residence was coded as ONE TRAIT with THREE STATES
  Matrilocal, patrilocal, neolocal
  We allowed for mixed strategies e.g. MP = ambilocal and main/alternative forms

- Used Multistate in BayesTraits to infer ancestral states and the parameters of the most likely model of evolution
  Tested our hypotheses over a posterior sample of 1000 trees
  Used reversible-jump MCMC procedure to help find the best model of evolution
  "Fossilised" early nodes to each possible state to test robustness

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

The evolution of marital residence
What did we do?

- Used independently-derived lexical phylogenies of AN and IE
  Matched ethnographic descriptions to linguistic groups

- Data on residence was coded as ONE TRAIT with THREE STATES
  Matrilocal, patrilocal, neolocal
  We allowed for mixed strategies e.g. MP = ambilocal and main/alternative forms

- Used Multistate in BayesTraits to infer ancestral states and the parameters of the most likely model of evolution
  Tested our hypotheses over a posterior sample of 1000 trees
  Used reversible-jump MCMC procedure to help find the best model of evolution
  "Fossilised" early nodes to each possible state to test robustness

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

indo-european

requires a two-rate model

infer patrilocality for PIE

austronesian

requires a three-rate model

infer matrilocality for PMP

The evolution of marital residence
What did we conclude?

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

The evolution of marital residence
What did we conclude?

- Commonalities in process:
  - Unstable matrilocality
  - Rare loss of patrilocality once gained

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

The evolution of marital residence
What did we conclude?

- Commonalities in process:
  Unstable matrilocality
  Rare loss of patrilocality once gained

- Differences in pattern and process:
  Require different number of rates of trait change (IE = 2, AN = 3)
  Different starting points

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

The evolution of marital residence
What did we conclude?

- Commonalities in process:
  Unstable matrilocality
  Rare loss of patrilocality once gained

- Differences in pattern and process:
  Require different number of rates of trait change (IE = 2, AN = 3)
  Different starting points

- Coding procedure can affect robustness
  For AN, including neolocality and considering prevailing/alternative forms means
  that PAN is less securely inferred to be matrilocal (though PMP still robust).

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

The evolution of marital residence
What did we conclude?

- Commonalities in process:
  Unstable matrilocality
  Rare loss of patrilocality once gained

- Differences in pattern and process:
  Require different number of rates of trait change (IE = 2, AN = 3)
  Different starting points

- Coding procedure can affect robustness
  For AN, including neolocality and considering prevailing/alternative forms means
  that PAN is less securely inferred to be matrilocal (though PMP still robust).

- *"Asking the same questions in different ethnographic regions heralds a useful*

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

Correlated change and coevolution

Correlated change and coevolution

Krebs & Davies 1992

Correlated change and coevolution

- Why are evolving traits correlated?

    1. The "correlation" imposed by the phylogeny (Galton's Problem)
    2. Repeated instances of changing together = *correlated change*
       Could be due to a third variable
       Or the characters being part of a suite of dependent characters
    3. Repeated instances of changing together
       that is due to one character influencing another = *coevolution*

Krebs & Davies 1992

Correlated change and coevolution

- Why are evolving traits correlated?

    1. The "correlation" imposed by the phylogeny (Galton's Problem)
    2. Repeated instances of changing together = *correlated change*
       Could be due to a third variable
       Or the characters being part of a suite of dependent characters
    3. Repeated instances of changing together
       that is due to one character influencing another = *coevolution*

- Comparative methods originally proposed as a way to assess the cross-species evidence for adaptation, along with:
  - experimental manipulations
  - observational studies
  - optimality modelling

Krebs & Davies 1992

a b c d e f g h

a
b
c
d
e
f
g
h

Correlated change between discrete characters

Standard correlation/regressions are for continuous characters

Assess the degree to which a unit of change in X predicts a unit of change in Y.

Correlated change between discrete characters

Standard correlation/regressions are for continuous characters

Assess the degree to which a unit of change in X predicts a unit of change in Y.

Correlated change between discrete characters

Standard correlation/regressions are for continuous characters

Assess the degree to which a unit of change in X predicts a unit of change in Y.

Discrete characters have traditionally been tested for correlation using contingency tables and chi-square tests

BUT Galton's Problem!

	post	pre
OV	15	4
VO	2	26

Co-occurences of evolutionary events not co-occurences of traits

- Ridley's method (1983)
- Concentrated changes (Maddison 1990)
- Pagel's method (1994)

Table 4.4 Lekking and sexual dimorphism in size and plumage in birds. Each data point represents a single species. The associations between lekking and size and plumage dimorphism are both significant at $P<0.001$ in this comparison with species counted as independent points. (After Höglund 1989).

Mating system	Sexual size dimorphism		Plumage dimorphism	
	Present	Absent	Present	Absent
Lekking	69	18	55	33
Non-lekking	13	13	8	18

Ord & Martins 2010 / Nunn 2011

Co-occurences of evolutionary events not co-occurences of traits

- Ridley's method (1983)
- Concentrated changes (Maddison 1990)
- Pagel's method (1994)

Table 4.4 Lekking and sexual dimorphism in size and plumage in birds. Each data point represents a single species. The associations between lekking and size and plumage dimorphism are both significant at $P<0.001$ in this comparison with species counted as independent points. (After Höglund 1989).

Mating system	Sexual size dimorphism		Plumage dimorphism	
	Present	Absent	Present	Absent
Lekking	69	18	55	33
Non-lekking	13	13	8	18

Ord & Martins 2010 / Nunn 2011

Co-occurences of evolutionary events not co-occurences of traits

- Ridley's method (1983)
- Concentrated changes (Maddison 1990)
- Pagel's method (1994)

3 changes in lekking
3 changes in dimorphism
NONE changing together

Table 4.4 Lekking and sexual dimorphism in size and plumage in birds. Each data point represents a single species. The associations between lekking and size and plumage dimorphism are both significant at $P<0.001$ in this comparison with species counted as independent points. (After Höglund 1989).

Mating system	Sexual size dimorphism		Plumage dimorphism	
	Present	Absent	Present	Absent
Lekking	69	18	55	33
Non-lekking	13	13	8	18

Ord & Martins 2010 / Nunn 2011

Discrete

A model-based method for correlated change

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

Pagel 1994 / Pagel & Meade 2004

Discrete
A model-based method for correlated change

- Allows for tests of directionality when used in conjunction with ancestral state inference

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

Pagel 1994 / Pagel & Meade 2004

Discrete
A model-based method for correlated change

- Allows for tests of directionality when used in conjunction with ancestral state inference

- Takes TWO binary-coded traits that have TWO states each

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

Pagel 1994 / Pagel & Meade 2004

Discrete
A model-based method for correlated change

- Allows for tests of directionality when used in conjunction with ancestral state inference

- Takes TWO binary-coded traits that have TWO states each

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

- We infer the Lh of two models

INDEPENDENT:

the traits change their state independent of the other trait and states
i.e. changes in trait A are not affected by changes in trait B

DEPENDENT:

Pagel 1994 / Pagel & Meade 2004

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

independent model

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

independent model

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

independent model

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

independent model

	post	pre
OV	15	4
VO	2	26

dependent model

OV
POSTPOSITION

OV
PREPOSITION

	post	pre
OV	15	4
VO	2	26

VO
POSTPOSITION

VO
PREPOSITION

dependent model

OV
POSTPOSITION

OV
PREPOSITION

VO
POSTPOSITION

VO
PREPOSITION

(in)dependent model

OV
POSTPOSITION 1

OV
PREPOSITION 2

VO
POSTPOSITION 3

VO
PREPOSITION 4

(in)dependent model

(in)dependent model

one sort of **dependent** model

one sort of **dependent** model

another sort of **dependent** model

Discrete in a Bayesian MCMC framework

Discrete in a Bayesian MCMC framework

- Bayesian approach allows us to incorporate uncertainty:

  Phylogenetic uncertainty: by using a posterior distribution of trees

  Character uncertainty: by incorporating probabilistic models of evolution

  Model uncertainty: gives us distributions of the rate parameters

Discrete in a Bayesian MCMC framework

- Bayesian approach allows us to incorporate uncertainty:
  Phylogenetic uncertainty: by using a posterior distribution of trees
  Character uncertainty: by incorporating probabilistic models of evolution
  Model uncertainty: gives us distributions of the rate parameters

- **PROCEDURE**: Run both dependent and independent models
  If dependent model has higher likelihood, then prefer over independent.
  - Examine dynamics of change in dependent model, incorporating ancestral state estimates if known.
  - Compare dynamics of models across lineages/families.
  - Test the robustness of the model with fossilisation or model-specification.
  - Decide to what extent uncertainty impacts your confidence in the inferences.

Word-order across language families

postposition
preposition
object-verb
verb-object

Dunn *et al* 2011 *Nature*

Word-order across language families

Dunn *et al* 2011 *Nature*

Word-order across language families

Dunn *et al* 2011 *Nature*

Word-order across language families

Evolved structure of language shows lineage-specific trends in word-order universals

Michael Dunn[1,2], Simon J. Greenhill[3,4], Stephen C. Levinson[1,2] & Russell D. Gray[3]

Language families: previously a problem for sampling approaches, now crucial resources

Dunn *et al* 2011 *Nature*

Word-order across language families

Evolved structure of language shows lineage-specific trends in word-order universals

Michael Dunn[1,2], Simon J. Greenhill[3,4], Stephen C. Levinson[1,2] & Russell D. Gray[3]

Language families: previously a problem for sampling approaches, now crucial resources

Dunn *et al* 2011 *Nature*

Coevolutionary test
Bantu descent and mode of subsistence

Is patriliny (descent following a male lineage) associated with the acquisition of heritable resources that individual men can monopolise?

"The cow is the enemy of matriliny"

Holden & Mace 2003

Bantu descent and mode of subsistence

- Independently-derived lexical phylogenies of cognate-coded Bantu basic vocabulary (n=68)

- Coded ethnographic data

Holden & Mace 2003

Bantu descent and mode of subsistence

- Independently-derived lexical phylogenies of cognate-coded Bantu basic vocabulary (n=68)

- Coded ethnographic data

	cattle	no cattle
patrilineal	25	18
matrilineal	5	20

Holden & Mace 2003

Bantu descent and mode of subsistence

Matrilineal descent **Cattle present**	**Patrilineal descent** **Cattle present**
Matrilineal descent **Cattle absent**	**Patrilineal descent** **Cattle absent**

L_I= -62.52 L_D= -56.80 LR=5.72, p=0.02

Bantu descent and mode of subsistence

L_I= -62.52 L_D= -56.80 LR=5.72, p=0.02

Bantu descent and mode of subsistence

L_I= -62.52 L_D= -56.80 LR=5.72, p=0.02

Phylogeny and geography

Guglielmino et al 1995 PNAS / Mace & Jordan 2011 *Phil. Trans Roy Soc London B*

geographic and phylogenetic nearest neighbours

Guglielmino et al 1995 PNAS / Mace & Jordan 2011 *Phil. Trans Roy Soc London B*

geographic and phylogenetic nearest neighbours

Guglielmino et al 1995 PNAS / Mace & Jordan 2011 *Phil. Trans Roy Soc London B*

geographic and phylogenetic nearest neighbours

Guglielmino et al 1995 PNAS / Mace & Jordan 2011 *Phil. Trans Roy Soc London B*

geographic and phylogenetic nearest neighbours

Guglielmino et al 1995 PNAS / Mace & Jordan 2011 *Phil. Trans Roy Soc London B*

Across 80 Austronesian societies
for each of 37 social structure traits
and 29 economic traits:
What best predicts the cultural trait a society has?

Is it your geographical neighbour?
or your phylogenetic sister?

Mace & Jordan 2011 *Phil. Trans Roy Soc London B.*

Mace & Jordan 2011 *Phil. Trans Roy Soc London B.*

PNN: heritable resources

Mace & Jordan 2011 *Phil. Trans Roy Soc London B.*

Mace & Jordan 2011 *Phil. Trans Roy Soc London B.*

Mace & Jordan 2011 *Phil. Trans Roy Soc London B.*