

Phylogenetic Signal

3 February 2017

SESYNC

What is phylogenetic signal and who cares?

- The tendency for closely related species to have similar properties (traits, niches, etc).

What is phylogenetic signal and who cares?

- The tendency for closely related species to have similar properties (traits, niches, etc).
- *"As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera... We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature; but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life."*

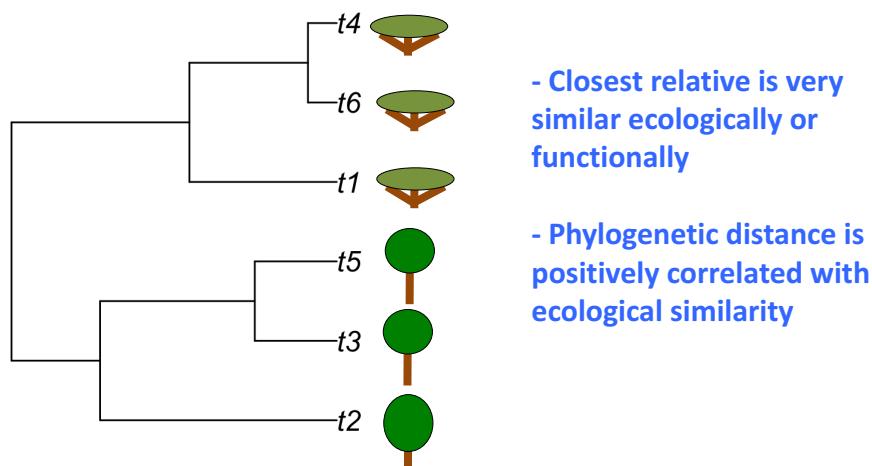
What is phylogenetic signal and who cares?

- The tendency for closely related species to have similar properties (traits, niches, etc).
- Why some view signal is a statistical nuisance it may explain a lot of the natural patterns we see today

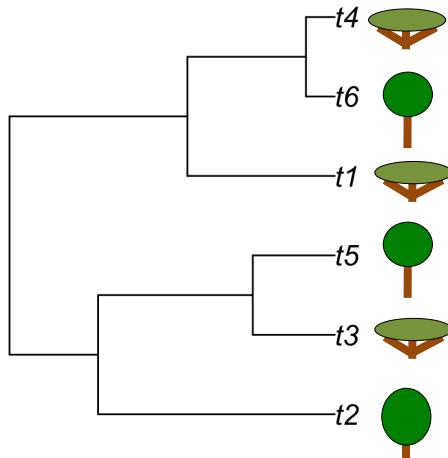
What is phylogenetic niche conservatism and how is it related to phylogenetic signal?

- Conceptually these may sound similar, but...what are we really talking about here?
- PNC has been used in a variety of ways from sister lineages having NO divergence in niches to sister lineages being more similar than expected in their niches.
- Most quantitative measures of phylogenetic signal measure similarity and not stasis
- HIGHLY recommend Blomberg & Garland 2002 J of Evolutionary Biology

Phylogenetic Signal

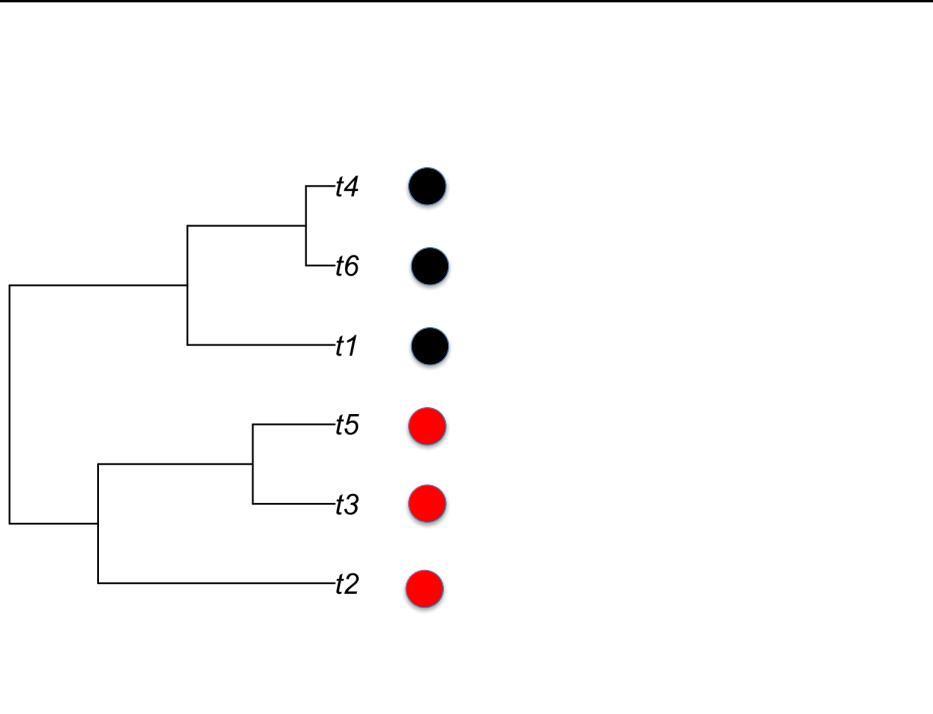


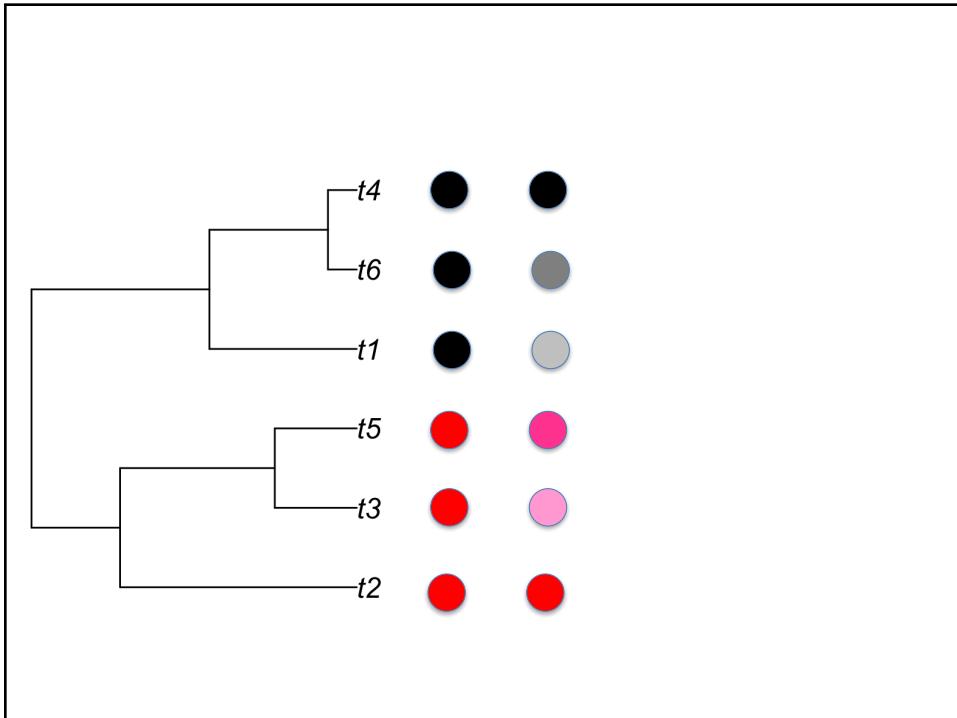
NO Phylogenetic Signal



Closest relative is very different ecologically or functionally

Phylogenetic distance is not correlated or negatively correlated with ecological similarity





Is phylogenetic signal or PNC common/important?

- Some have argued that it is not common and must be proven (not assumed).
 - The researchers are often those that study adaptive evolution and adaptive radiation

VOL. 177, NO. 6 THE AMERICAN NATURALIST JUNE 2011

Seeing the Forest for the Trees: The Limitations of Phylogenies in Comparative Biology

(American Society of Naturalists Address)*

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Is phylogenetic signal or PNC common/important?

- Others argue that PNC or signal is very common and fundamentally important for understanding ecological patterns

ECOLOGY LETTERS

Ecology Letters, (2010) 13: 1310–1324 doi: 10.1111/j.1461-0248.2010.01515.x

REVIEW AND SYNTHESIS

Niche conservatism as an emerging principle in ecology and conservation biology

Abstract
 The diversity of life is ultimately generated by evolution, and much attention has focused on the rapid evolution of ecological traits. Yet, the tendency for many ecological traits to instead remain similar over time [niche conservatism (NC)] has important consequences for the way we think about species interactions and their role in ecology and conservation biology. Here, we describe the mounting evidence for the importance of NC to major topics in ecology (e.g. species richness, ecosystem function) and conservation (e.g. climate change, invasive species). We also review other areas where it may be important but has generally been overlooked, in both ecology (e.g. food webs, disease ecology, mutualistic interactions) and conservation (e.g. habitat modification). We summarize methods for testing for NC, and suggest that a commonly used and advocated method (involving a test for phylogenetic signal) is potentially problematic, and describe alternative

Why May PNC Be Important For Ecology? – One Example

- Latitudinal Gradient in Diversity

Review *TRENDS in Ecology and Evolution* Vol.19 No.12 December 2004 Full text provided by www.sciencedirect.com

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Historical biogeography, ecology and species richness

John J. Wiens¹ and Michael J. Donoghue²

¹Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794-5245, USA

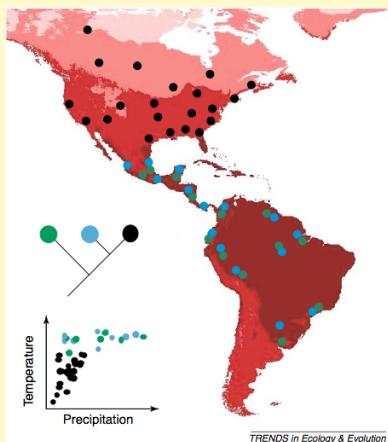
²Department of Ecology and Evolutionary Biology and Peabody Museum of Natural History, Yale University, New Haven, CT 06511, USA

Why May PNC Be Important For Ecology? – One Example

Box 2. Phylogenetic niche conservatism and niche evolution

Phylogenetic niche conservatism [27,44,47,48] can be a crucial factor in explaining large-scale patterns of distribution. The fundamental niche of a species describes the abiotic conditions in which it can persist and maintain viable populations [49]. We specifically refer to the geographical range, rather than other aspects of the niche (e.g. diet). Although organisms collectively occupy a wide range of environmental conditions on Earth, most species and clades occupy only a limited subset of these. This set of acceptable conditions can be determined by intrinsic organismal traits, such as physiology, and can be maintained over long evolutionary timescales. For example, many groups of organisms are globally widespread in tropical regions, but have not successfully invaded or radiated in temperate regions, despite tens or hundreds of millions of years of opportunity (e.g. onychophorans, cycads and caecilians). If there is niche conservatism within a clade, then the ancestral niche can determine the regions and habitats to which the clade can spread, and those in which it will persist in the face of environmental change. Although niche conservatism can be seen as a pattern or outcome rather than a process, it can be actively maintained by microevolutionary forces over time [27].

Niche evolution (i.e. the expansion of niche breadth or specialization for new conditions) should enable invasion of new habitats and climatic regimes that had previously limited the distribution of a clade (Figure 1). Even though certain niche characteristics might be shared by all members of a clade through phylogenetic descent, niche evolution can only occur in individual species. Thus, changes in niche breadth in one species in one part of the range of a clade might have only a limited impact on the overall distribution of the clade. We think that the interplay between niche conservatism and niche evolution will prove to be a major theme in the biogeographical history of



TRENDS in Ecology & Evolution

Why May PNC Be Important For Ecology? – One Example

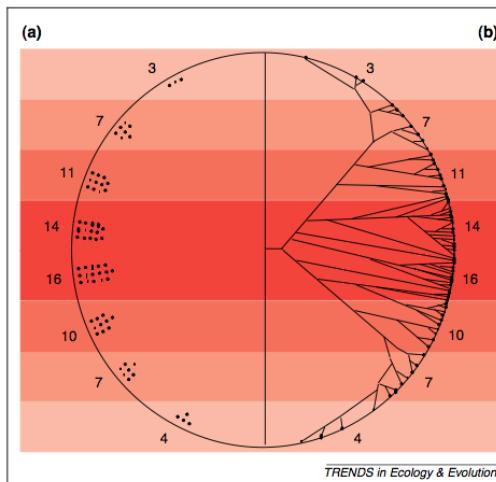


Figure 1. Two approaches to the problem of explaining global patterns of species richness. Standard ecological approaches (a) seek correlations between the

Why May PNC Be Important For Ecology? – A Real Example

Journal of Biogeography (J. Biogeogr.) (2006) **33**, 770–780



Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds

Bradford A. Hawkins^{1*}, José Alexandre Felizola Diniz-Filho², Carlos A. Jaramillo³ and Stephen A. Soeller⁴

Why May PNC Be Important For Ecology? – A Real Example

Niche conservatism and bird diversity

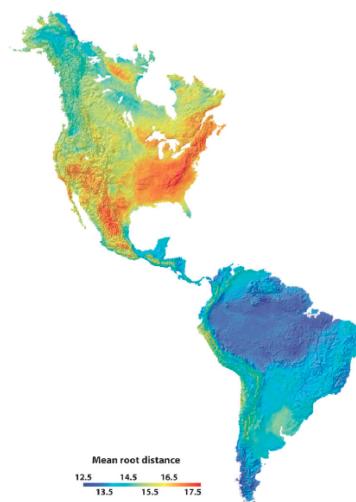


Figure 2 Geographical pattern of bird mean root distance (MRD), resolved to family and based on a combination of Sibley & Ahlquist's (1990) phylogeny for non-passerines and Barker *et al.*'s (2004) phylogeny for passerines. Grain size as in Fig. 1.

Why May PNC Be Important For Ecology? – A Real Example

- Peterson et al. 1999 Science

Conservatism of Ecological Niches in Evolutionary Time

A. T. Peterson,^{1*} J. Soberón,² V. Sánchez-Cordero³

Theory predicts low niche differentiation between species over evolutionary time scales, but little empirical evidence is available. Reciprocal geographic predictions based on ecological niche models of sister taxon pairs of birds, mammals, and butterflies in southern Mexico indicate niche conservatism over several million years of independent evolution (between putative sister taxon pairs) but little conservatism at the level of families. Niche conservatism over such time scales indicates that speciation takes place in geographic, not ecological, dimensions and that ecological differences evolve later.

Why May PNC Be Important For Ecology? – A Real Example

- Pairs of species
- Use ecological niche model for one species to predict the range of the other species

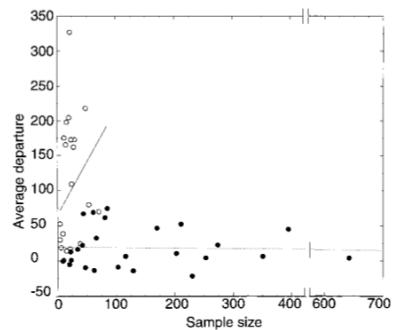


Fig. 2. Graph of average departure in reciprocal predictions among putative sister taxon pairs (open symbols) and confamilial species pairs (filled symbols), illustrating the significant interpredictiveness among sister taxa and the nonsignificant interpredictiveness among distantly related, confamilial taxa. Vertical axis

Some examples of no phylogenetic signal

- Anolis lizards in Caribbean (Losos et al. 1998 Science)

Contingency and Determinism in Replicated Adaptive Radiations of Island Lizards

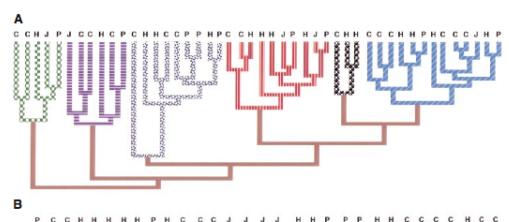
Jonathan B. Losos,* Todd R. Jackman, Allan Larson,
Kevin de Queiroz, Lourdes Rodríguez-Schettino

Some examples of no phylogenetic signal

Contingency and Determinism in Replicated Adaptive Radiations of Island Lizards

Jonathan B. Losos,* Todd R. Jackman, Allan Larson,
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A = Trait dendrogram



B

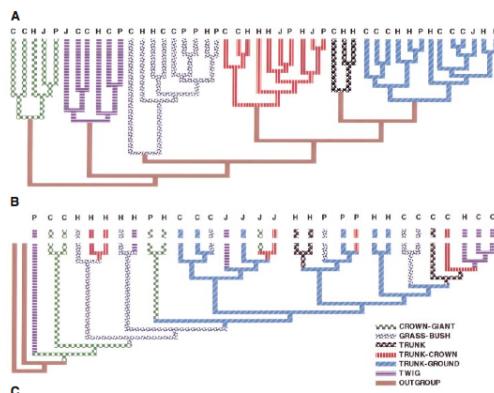
Some examples of no phylogenetic signal

Contingency and Determinism in Replicated Adaptive Radiations of Island Lizards

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A = Trait dendrogram

B = Phylogeny



Some examples of no phylogenetic signal

Contingency and Determinism in Replicated Adaptive Radiations of Island Lizards

Jonathan B. Losos,* Todd R. Jackman, Allan Larson,
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A = Trait dendrogram

B = Phylogeny

C= Phylogeny on each island

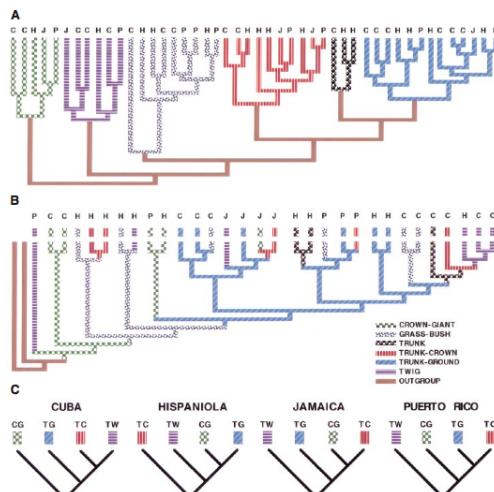


Fig. 1. (A) UPGMA phenogram showing that members of the same ecomorph class cluster in morpho-

Some examples of no phylogenetic signal

- Spiders in Hawaii

Some examples of no phylogenetic signal

- Spiders in Hawaii (Gillespie 2004 Science)

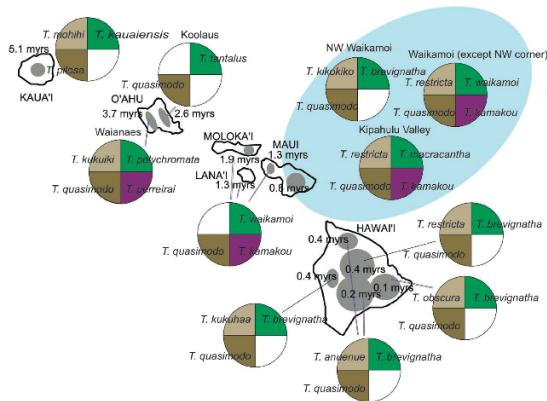
Community Assembly Through Adaptive Radiation in Hawaiian Spiders

Rosemary Gillespie

Communities arising through adaptive radiation are generally regarded as unique, with speciation and adaptation being quite different from immigration and ecological assortment. Here, I use the chronological arrangement of the Hawaiian Islands to visualize snapshots of evolutionary history and stages of community assembly. Analysis of an adaptive radiation of habitat-associated, polychromatic spiders shows that (i) species assembly is not random; (ii) within any community, similar sets of ecomorphs arise through both dispersal and evolution; and (iii) species assembly is dynamic with maximum species numbers in communities of intermediate age. The similar patterns of species accumulation through evolutionary and ecological processes suggest universal principles underlie community assembly.

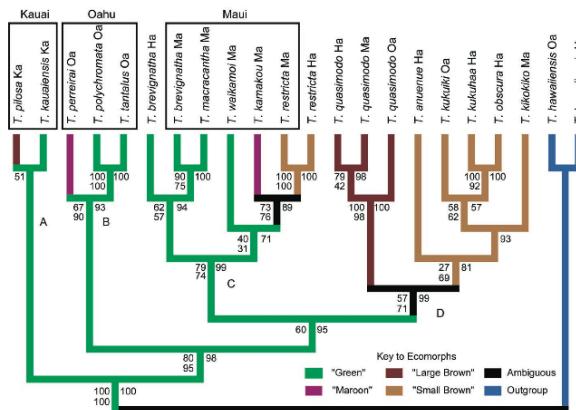
Some examples of no phylogenetic signal

- Spiders in Hawaii (Gillespie 2004 Science)



Some examples of no phylogenetic signal

- Spiders in Hawaii (Gillespie 2004 Science)



Measuring Signal

How do we measure “phylogenetic signal”

- Oldest method is hierarchical variance partitioning via a nested ANOVA
- How much variance is explained at the order/family/genus/species level.

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- How much variance is explained at the order/family/genus/species level.

VOL. 168, NO. 4 THE AMERICAN NATURALIST OCTOBER 2006

E-ARTICLE

Phylogenetic and Growth Form Variation in the Scaling of Nitrogen and Phosphorus in the Seed Plants

Andrew J. Kerkhoff,^{1,*} William F. Fagan,^{2,†} James J. Elser,^{3,‡} and Brian J. Enquist^{1,§}

How do we measure “phylogenetic signal”

VOL. 168, NO. 4 THE AMERICAN NATURALIST OCTOBER 2006

E-ARTICLE

Phylogenetic and Growth Form Variation in the Scaling of Nitrogen and Phosphorus in the Seed Plants

Andrew J. Kerkhoff,^{1,*} William F. Fagan,^{2,†} James J. Elser,^{3,‡} and Brian J. Enquist^{1,§}

Table A3: Phylogenetic signal and taxonomic partitioning of variance in stoichiometric traits

Organ	Phylogenetic signal		Nested variance components		
	Divergence SD	P	Family	Genus	Species (residual)
Leaf:					
N	.12 (326)	.001	.41 (134)	.32 (563)	.28 (973)
P	.18 (330)	.001	.38 (135)	.30 (566)	.32 (975)
N : P	.13 (288)	.001	.16 (125)	.35 (466)	.49 (790)
Stem:					
N	.16 (124)	.001	.42 (64)	.33 (158)	.25 (247)
P	.26 (128)	.001	.31 (69)	.39 (146)	.30 (228)
N : P	.16 (109)	.001	.30 (62)	.26 (124)	.44 (192)
Root:					
N	.15 (116)	.001	.34 (60)	.25 (150)	.41 (229)
P	.24 (98)	.001	.43 (60)	.37 (119)	.20 (169)
N : P	.19 (94)	.001	.40 (58)	.25 (112)	.35 (161)
Reproductive:					
N	.14 (65)	.001	.38 (39)	.37 (101)	.25 (138)
P	.19 (52)	.02	.52 (39)	.17 (83)	.31 (101)
N : P	.14 (44)	.02	.36 (34)	.25 (65)	.38 (79)

How do we measure “phylogenetic signal”

- The obvious problem with this approach is that it relies on taxonomic ranks and not branch lengths.
 - Thus not commonly used any more

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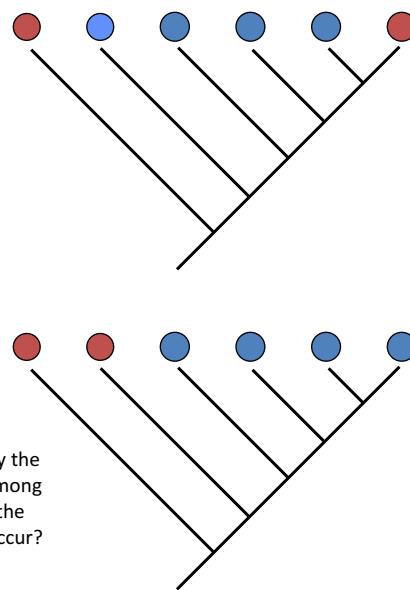
Andrew J. Kerkhoff,^{1,*} William F. Fagan,^{1,2} James J. Elser,^{3,4} and Brian J. Enquist^{1,5}

How do we measure “phylogenetic signal”

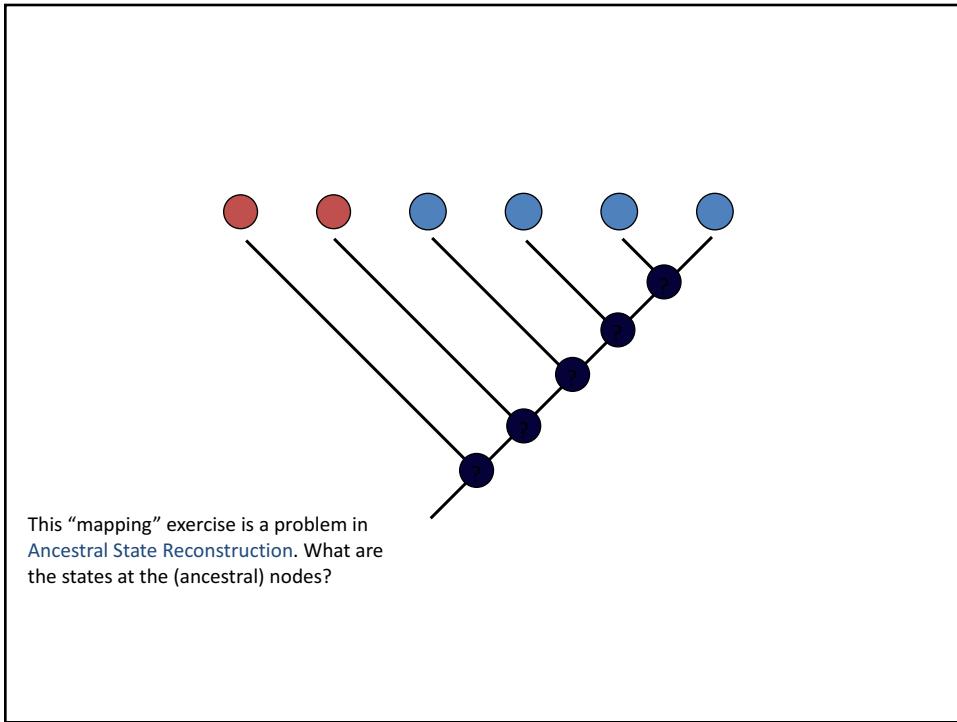
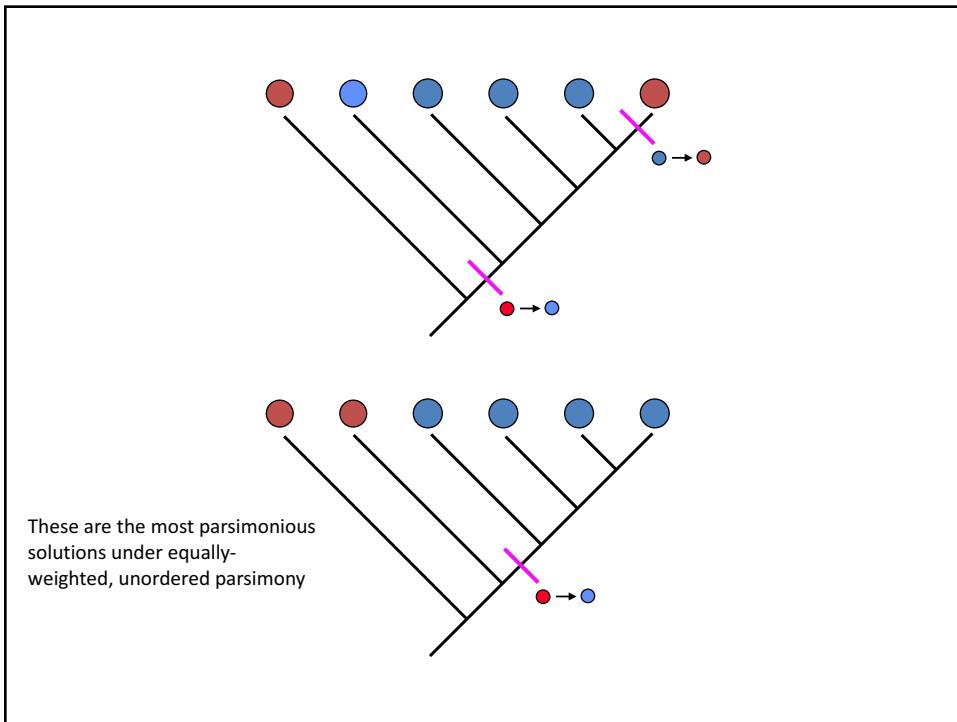
- A slightly more modern approach is to map a discrete character onto a phylogeny
 - Note the character wasn’t used to make the phylogeny!
- Quantify the minimum number of character state changes that must have occurred
- Compare this to a null expectation by shuffling names of species on the phylogeny

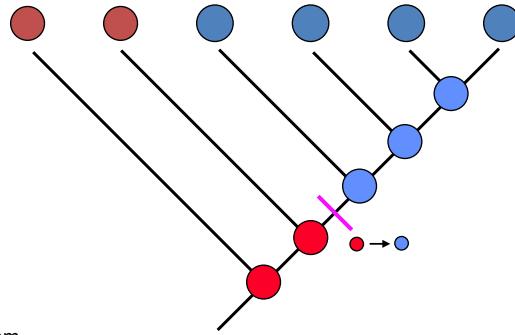
A 'Simple' Example

Consider the problem of estimating the historical pattern of changes in a character that can take two states, red and blue:

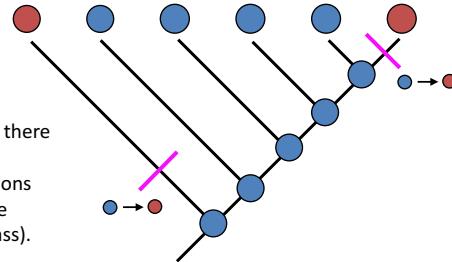
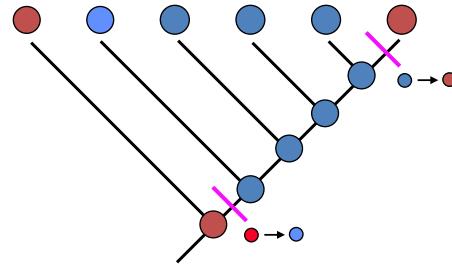


These two trees show only the pattern of relationships among the terminals. Where did the character-state changes occur?

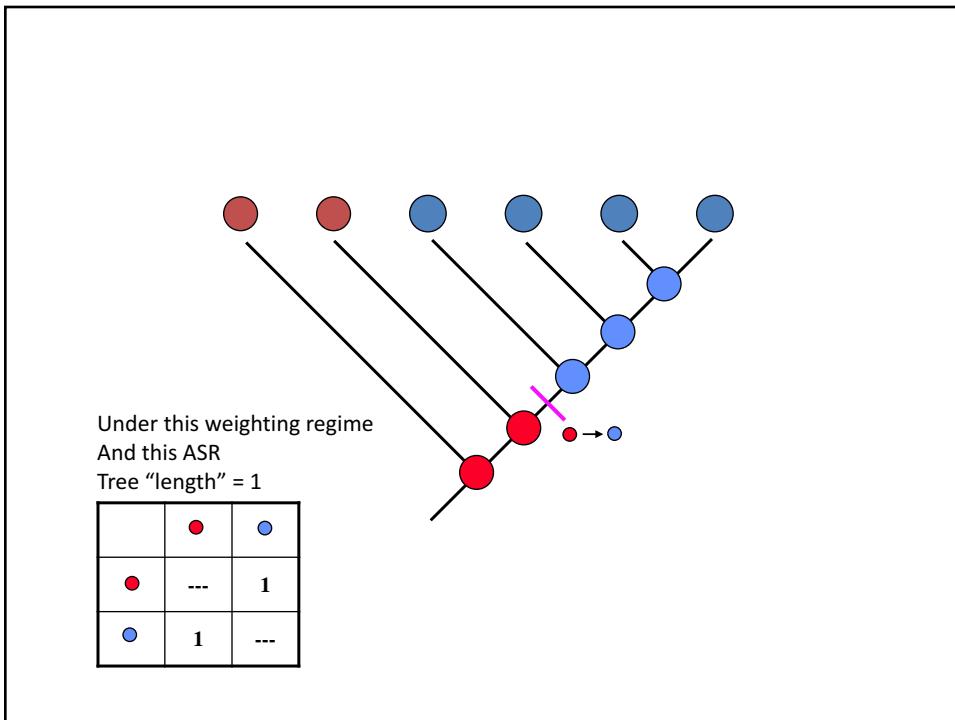
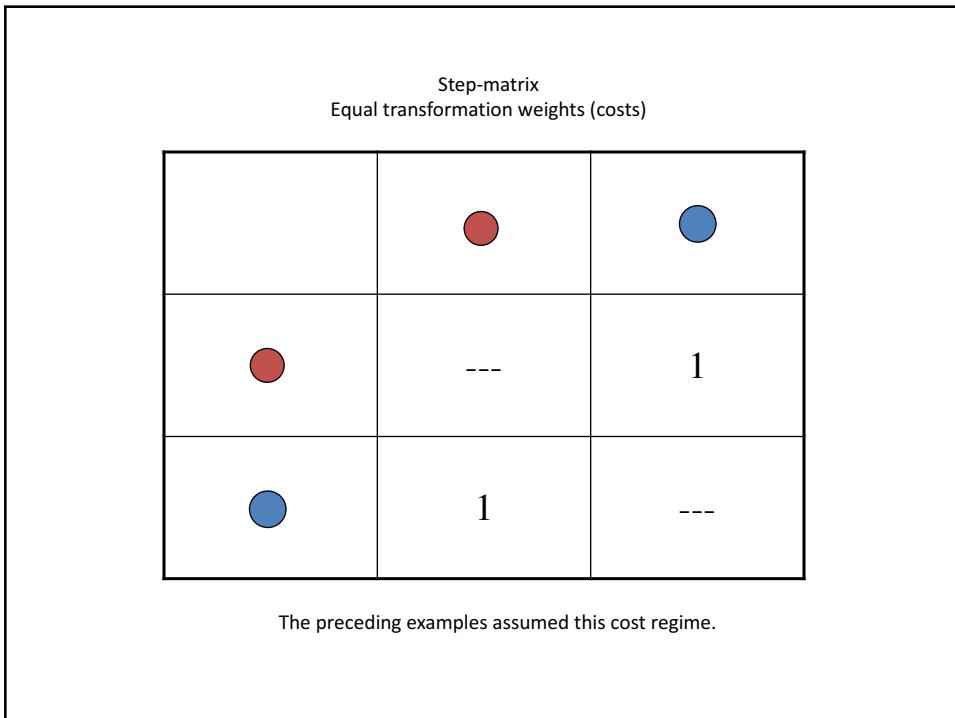


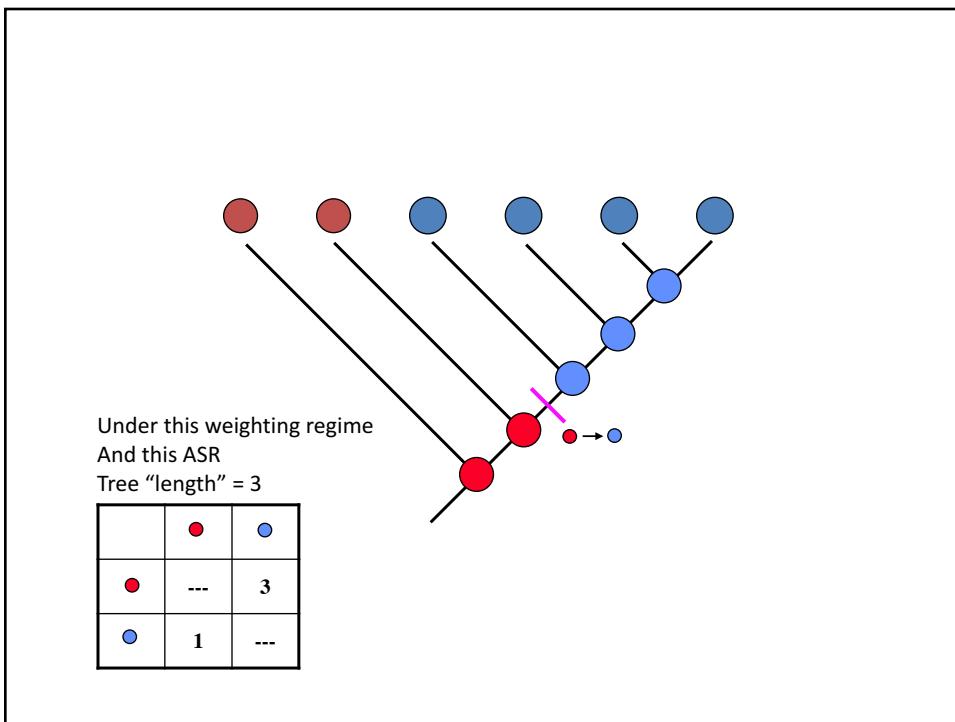
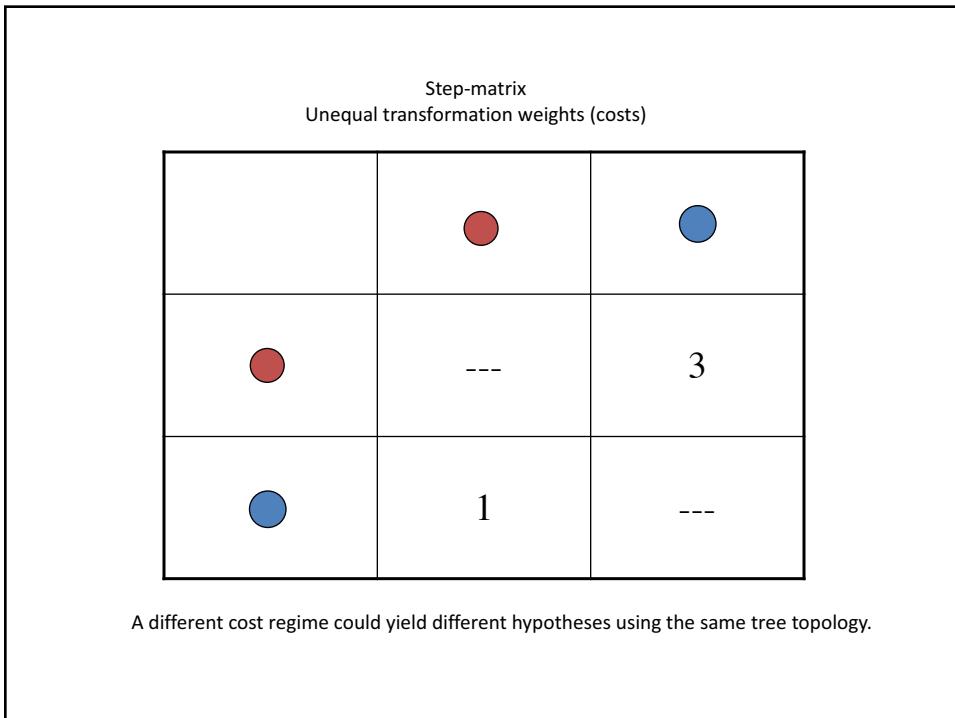


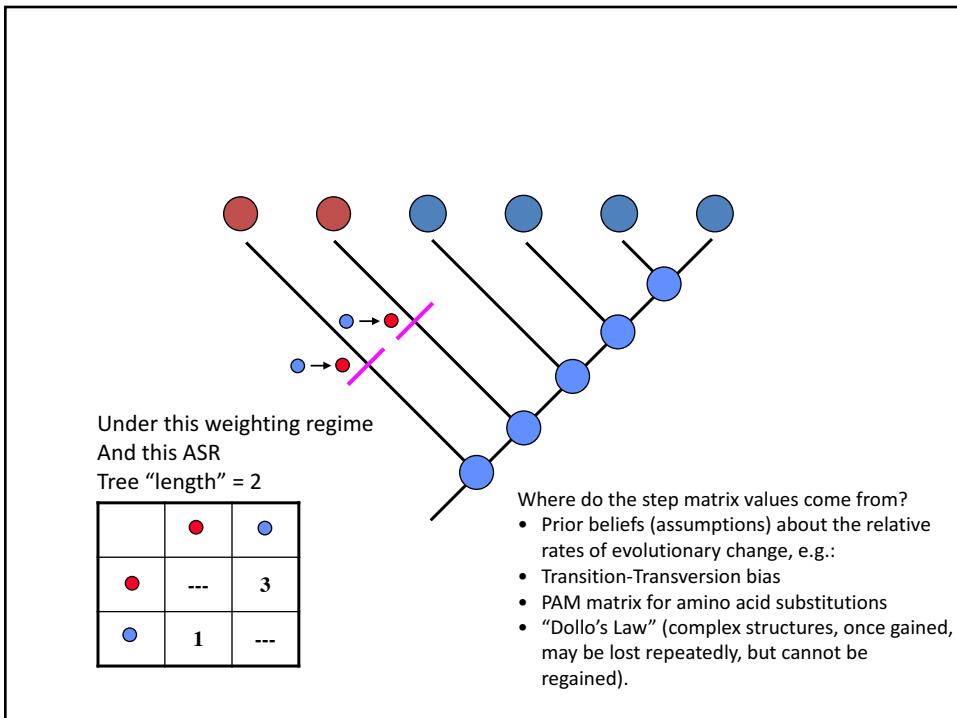
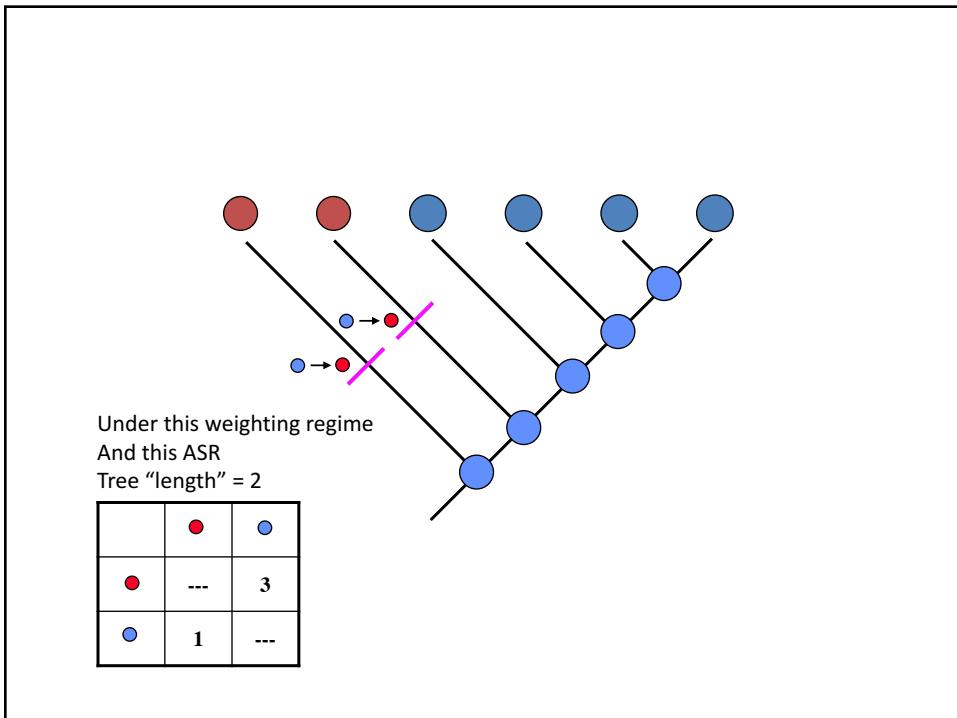
A more explicit diagram
indicating the hypothesis
suggested by our ASR exercise.



For a single tree topology, there
may be multiple equally
parsimonious reconstructions
(see 4-taxon unrooted tree
example from previous class).







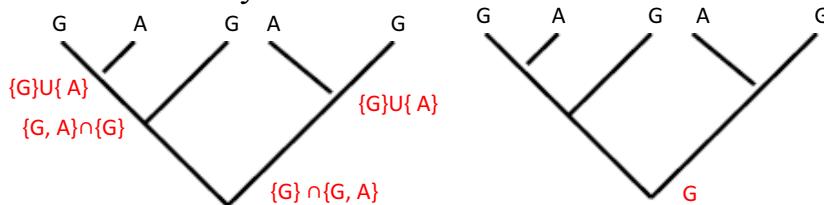
Ancestral States from Parsimony

- Fitch (parsimony) method

Step 1: Compute a subset S_x of letters for each node x with children y and z as follows

$$S_x = \begin{cases} S_y \cup S_z & \text{if } S_y \text{ and } S_z \text{ are disjoint} \\ S_y \cap S_z & \text{otherwise} \end{cases}$$

Step 2: Select a letter from the subset obtained at the root randomly.



How do we measure “phylogenetic signal”

- A slightly more modern approach is to map a discrete character onto a phylogeny
 - Note the character wasn't used to make the phylogeny!
- The problem with this is that not all traits are discrete

How do we measure “phylogenetic signal”

- A still frequently used approach is a Mantel Test
 - Trait distance matrix vs phylogenetic distance matrix

How do we measure “phylogenetic signal”

BRIEF COMMUNICATION

doi:10.1111/j.1558-5646.2010.00973.x

POOR STATISTICAL PERFORMANCE OF THE MANTEL TEST IN PHYLOGENETIC COMPARATIVE ANALYSES

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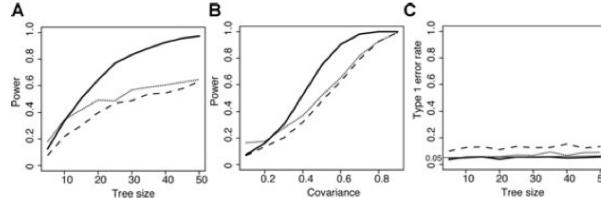


Figure 2. Statistical power (A & B) and type-I error (C) for phylogenetic tests of character correlation using the standard partial Mantel test (dashed line), PP Mantel test (dotted line), and independent contrasts (solid line). In each case, 1000 simulated datasets were analyzed for a range of tree sizes with an expected covariance of 0.5 (in A and C) or for trees with 25 taxa and a range of covariance values (B).

How do we measure “phylogenetic signal”

- Recent work has shown the Mantel approach to lack statistical power

BRIEF COMMUNICATION

doi:10.1111/j.1558-5646.2010.00973.x

POOR STATISTICAL PERFORMANCE OF THE MANTEL TEST IN PHYLOGENETIC COMPARATIVE ANALYSES

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How do we measure “phylogenetic signal”

- A popular method is called: “Blomberg’s K statistic” after Blomberg et al. 2003 Evolution
- Blomberg’s K statistic asks whether the observed trait variation on a phylogeny is smaller than expected given a Brownian motion model of trait evolution

Evolution, 57(4), 2003, pp. 717–745

TESTING FOR PHYLOGENETIC SIGNAL IN COMPARATIVE DATA: BEHAVIORAL TRAITS ARE MORE LABILE

SIMON P. BLOMBERG,¹ THEODORE GARLAND, JR.,^{1,2} AND ANTHONY R. IVES^{3,4}

¹Department of Biology, University of California, Riverside, California 92521

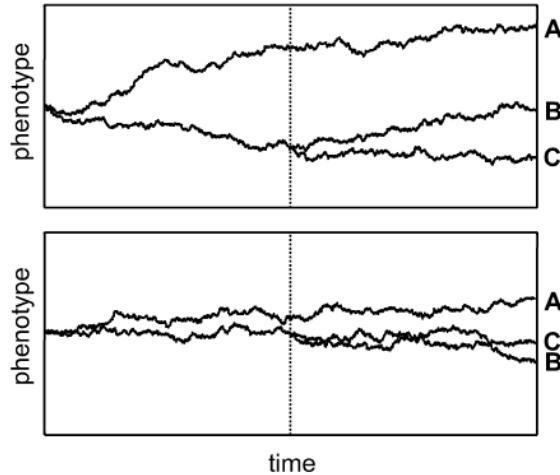
²E-mail: tgarland@citrus.ucr.edu

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Phylogenetic Signal and Brownian Motion Model of Trait Evolution

- Variance in traits should increase through time using a Brownian motion model of trait evolution (TOP)
- If there is Phylogenetic Signal we should have less variation in trait data than expected by Brownian motion model (BOTTOM)



Phylogenetic Signal and Brownian Motion Model of Trait Evolution

- More modern approaches simulate the expected trait distribution on the phylogeny
- Compare the observed distribution of traits to that model (usually Brownian) of trait evolution

Phylogenetic Signal and Brownian Motion Model of Trait Evolution

- So we must measure trait variance observed in the data
- Next we simulate trait evolution on the phylogenetic tree using a Brownian motion model of evolution and compare

K = Expected Variance / Observed Variance

Values < 1 indicate lower than expected variance aka “phylogenetic signal” or “phylogenetic conservatism”

Values > 1 indicate higher than expected variance aka NO “phylogenetic signal”

Phylogenetic Signal

- Example from Blomberg et al. 2003

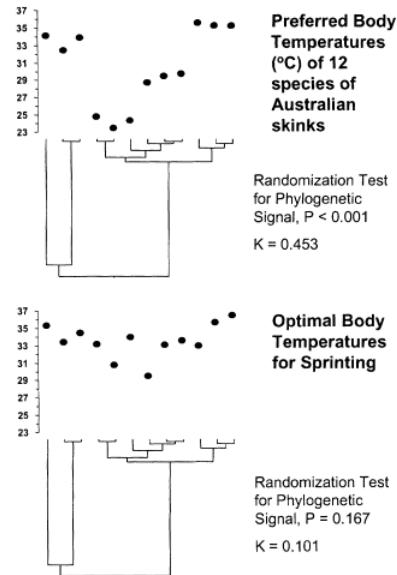
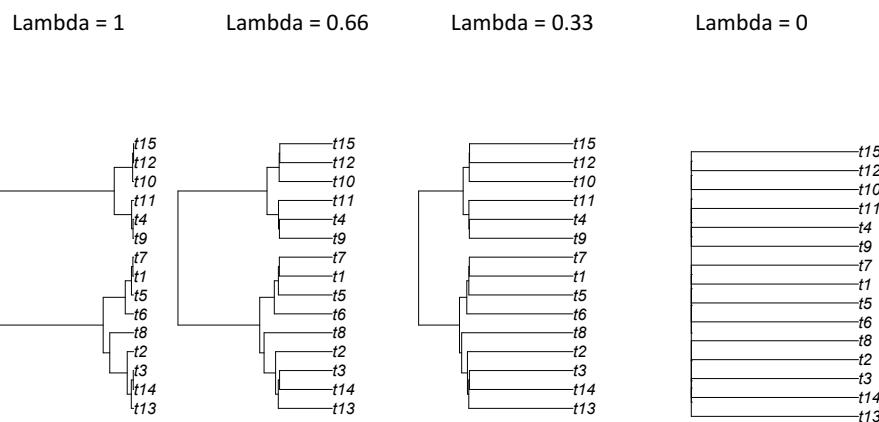


FIG. 4. Example in which significant phylogenetic signal is detected for one trait but not for another. (A) Preferred body temperature of some Australian skinks ($P < 0.001$, $K = 0.453$). (B) Optimal body temperature for sprinting ($P = 0.167$, $K = 0.101$). Data and tree are from Huey and Bennett (1987) and Garland et al. (1991), respectively.

A second method for measuring “phylogenetic signal”

- Pagel’s Lambda
- Multiplying the off-diagonal elements of vcv by a lambda value
- What transformation best fits trait data arrayed across tips
- Lambda closer to zero indicates less signal (zero = star phylogeny)

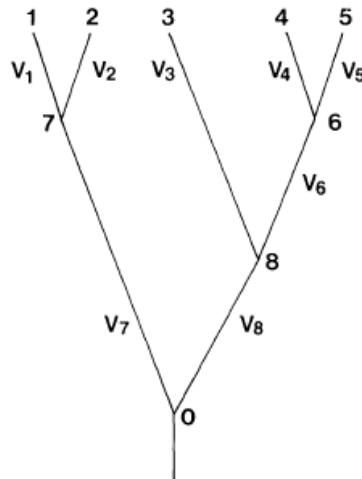


A final method for measuring “phylogenetic signal”

- Measure variance in node ‘contrasts’ and compare to that computed using randomized phylogenies

What are ‘node contrasts’

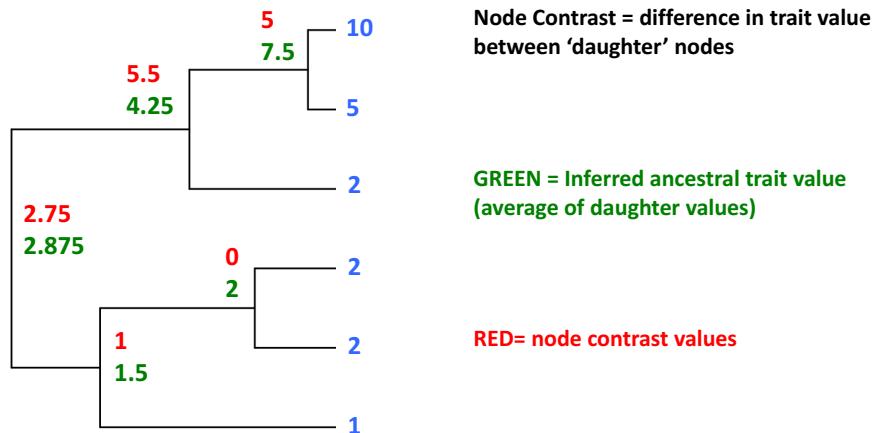
COMPARATIVE METHOD



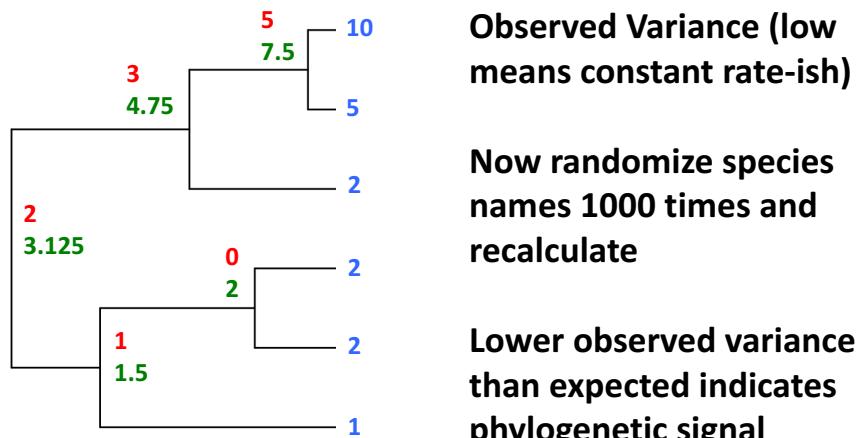
CONTRAST

$$\begin{aligned} X_1 - X_2 \\ X_4 - X_5 \\ X_3 - X_6 \\ X_7 - X_8 \end{aligned}$$

What are 'node contrasts'



Variance of 'node contrasts'



Divergences in Wood Density Along the Seed Plant Phylogeny

American Journal of Botany 94(3): 451–459. 2007.

ECOLOGICAL AND EVOLUTIONARY DETERMINANTS OF A KEY PLANT FUNCTIONAL TRAIT: WOOD DENSITY AND ITS COMMUNITY-WIDE VARIATION ACROSS LATITUDE AND ELEVATION¹

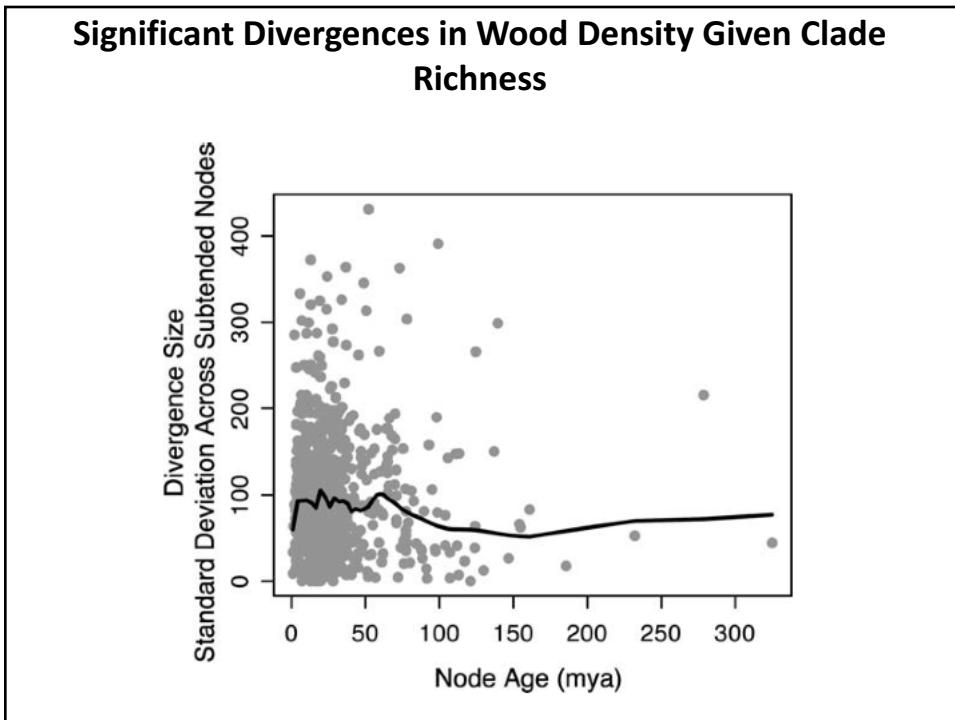
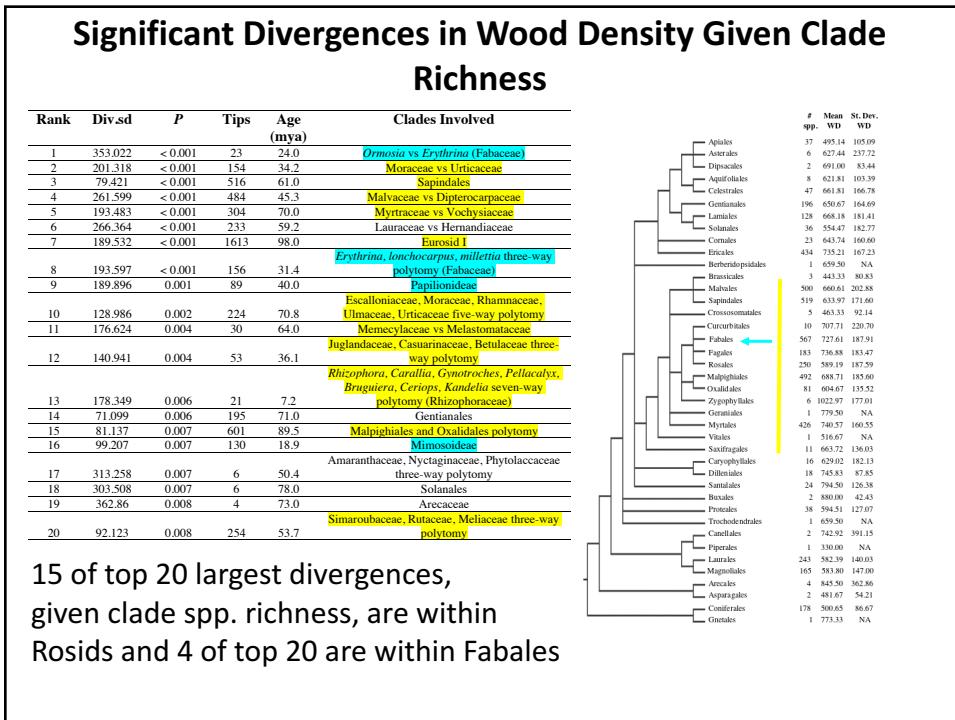
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Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA; and Center for Applied Biodiversity Science, Conservation International, Arlington, Virginia 22202 USA

METHODS - DIVERGENCES IN WOOD DENSITY

TRAIT CONSERVATISM AND DIVERGENCE

- Traits arrayed across the tips of the phylogeny.
- Divergence Width: A contrast
- Trait values randomized across the tips of the phylogeny 29,999 times
- Each iteration the Divergence Width was recorded to generate a null distribution
- Nodes with low quantile values = trait significantly conserved in subtended taxa
- Nodes with high quantile values = trait significantly divergent in subtended taxa



Divergences in Seed Mass Along the Seed Plant Phylogeny

A Brief History of Seed Size

Angela T. Moles,^{1,2*} David D. Ackerly,^{3†} Campbell O. Webb,⁴
John C. Tweddle,^{5,6} John B. Dickie,⁶ Mark Westoby²

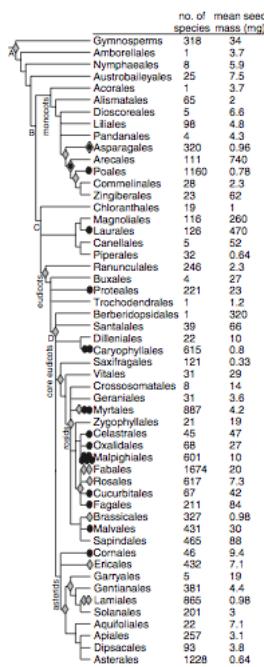
Improved phylogenies and the accumulation of broad comparative data sets have opened the way for phylogenetic analyses to trace trait evolution in major groups of organisms. We arrayed seed mass data for 12,987 species on the seed plant phylogeny and show the history of seed size from the emergence of the angiosperms through to the present day. The largest single contributor to the present-day spread of seed mass was the divergence between angiosperms and gymnosperms, whereas the widest divergence was between Celastraceae and Parnassiaceae. Wide divergences in seed size were more often associated with divergences in growth form than with divergences in dispersal syndrome or latitude. Cross-species studies and evolutionary theory are consistent with this evidence that growth form and seed size evolve in a coordinated manner.

Seed Mass – Moles et al. 2005 Science

- A global database of 13,000 seed mass values
- Question: when and where were the major evolutionary transitions in seed mass?
- Methods: Build a phylogenetic tree for all species in Phylomatic, measure divergence sizes and quantify significance with a null model

Seed Mass

- The group mapped major divergences onto the phylogeny
- Interestingly many of the clades that have major seed mass divergences also have the largest wood density divergences (even though these traits are not correlated)
- Suggests that functional diversity is disproportionately explained by large morphological divergences in a few clades



Divergences in Traits in a Forest Plot Community Phylogeny

Ecology, 90(8), 2009, pp. 2161–2170
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Opposing assembly mechanisms in a Neotropical dry forest:
implications for phylogenetic and functional community ecology

NATHAN G. SWENSON¹ AND BRIAN J. ENQUIST

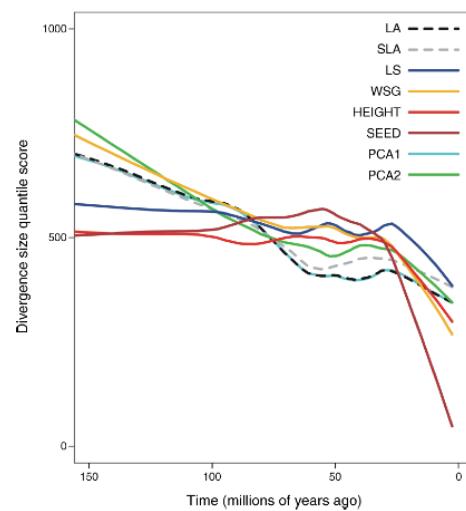
Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA

Trait evolution in a forest?

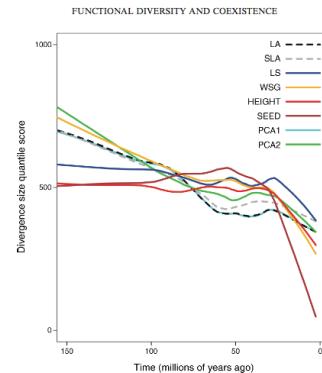
- We had measured phylogenetic and functional trait dispersion in this forest plot
- The patterns were not consistent and we wanted to know why
- The way to solve this was to map traits onto the community phylogeny and see where they diverge and the magnitude of that divergence

August 2009

FUNCTIONAL DIVERSITY AND COEXISTENCE



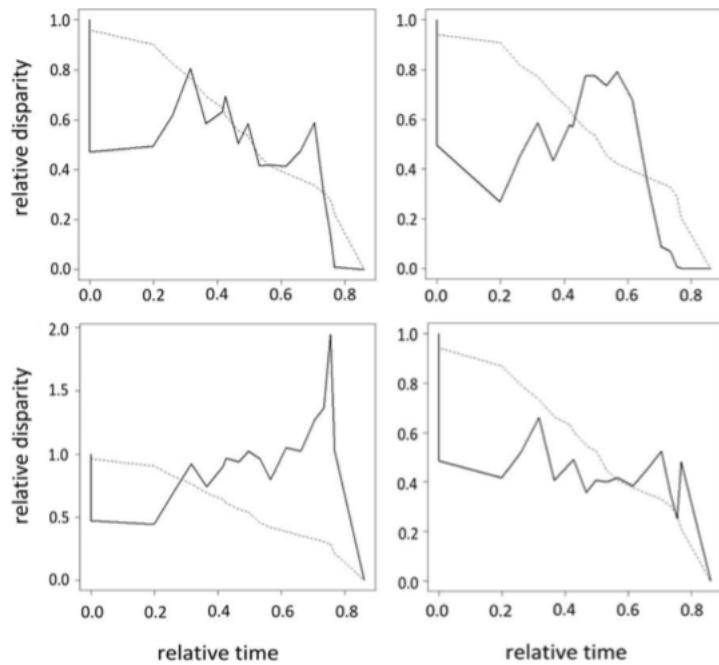
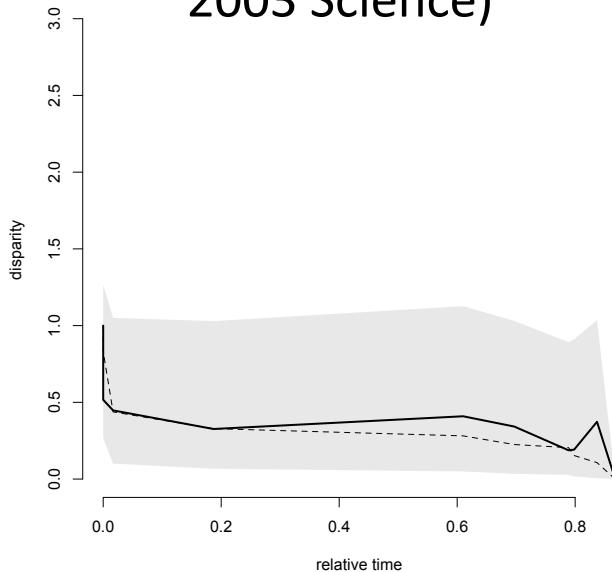
- Traits that had dispersion inconsistent with the phylogenetic dispersion tended to have larger divergences towards the tips of the phylogeny
- Thus for these traits mapping the phylogenetic pattern to the trait pattern is not possible or at least not easy.



Disparity through time (Harmon et al. 2003 Science)

- Measure disparity of species or daughter nodes for each internal node
- Compare to that expected given a model of trait evolution (eg BM)

Disparity through time (Harmon et al. 2003 Science)



Phylogenetic Eigenvectors

- Inputs a phylogenetic distance matrix into a PCA to decompose the phylo into many eigenvectors

