

Studying Evolutionary Ecology 2: Comparative Methods

Michael Noonan

Biol 417: Evolutionary Ecology



1. Housekeeping
2. Review
3. Comparative Methods
4. Phylogenetic Inertia
5. Limitations of comparative methods

Review

Experimentation, paired with design-based statistical inference, provides a powerful tool for understanding the mechanisms that drive evolutionary ecological phenomena.

Climbing the scientific ‘tree of progress’ via experimentation is an inherently slow process.

Not all questions/systems lend themselves to experimentation.

Today we will learn about the Comparative Method and how it provides a complementary approach to experimental ecology.

Comparative Methods

Comparative Methods



THE UNIVERSITY OF BRITISH COLUMBIA
Okanagan Campus



For some species, evolutionary processes can be studied via controlled experimentation (e.g., *E. coli*, *C. elegans*, *D. melanogaster*).



For some species, evolutionary processes can be studied via controlled experimentation (e.g., *E. coli*, *C. elegans*, *D. melanogaster*). For others, a measurable amount of evolution can take millennia to occur.



For some species, evolutionary processes can be studied via controlled experimentation (e.g., *E. coli*, *C. elegans*, *D. melanogaster*). For others, a measurable amount of evolution can take millennia to occur.

The question then is how do we study evolution in those species not amenable to experimentation?

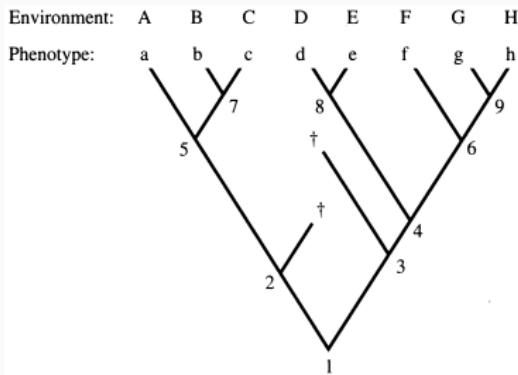
Comparative Methods



For some species, evolutionary processes can be studied via controlled experimentation (e.g., *E. coli*, *C. elegans*, *D. melanogaster*). For others, a measurable amount of evolution can take millennia to occur.

The question then is how do we study evolution in those species not amenable to experimentation?

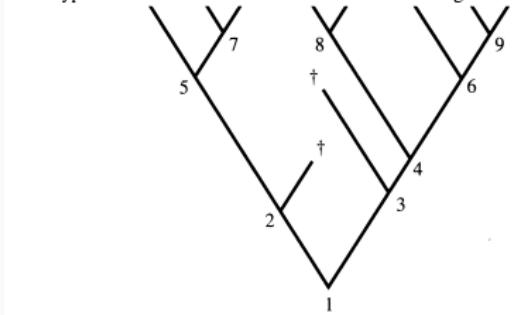
One solution is to treat individual species as the outcome of an experiment.



— Pianka 1999

Assuming species are adapted to their current environments, extant species can tell us something about their evolutionary history.

Environment: A B C D E F G H
Phenotype: a b c d e f g h

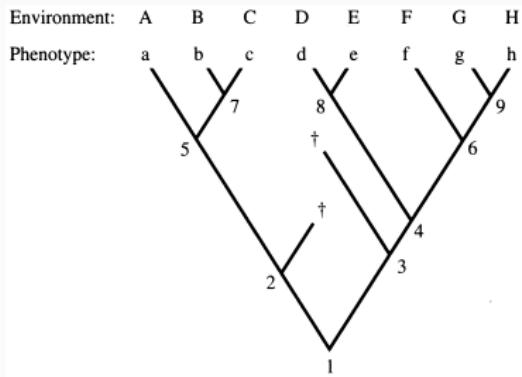


— Pianka 1999

Comparative Methods



Assuming species are adapted to their current environments, extant species can tell us something about their evolutionary history. E.g., when exposed to environment 'A', phenotype 'a' is observed, $B \rightarrow b$, $C \rightarrow c$, etc...

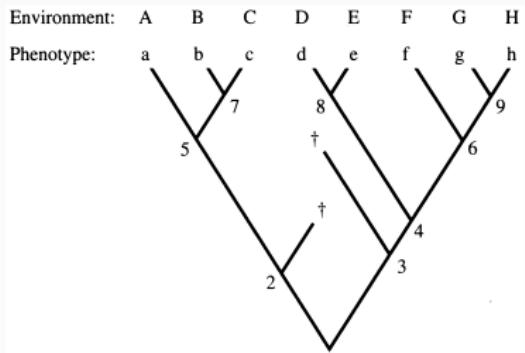


Comparative Methods



Assuming species are adapted to their current environments, extant species can tell us something about their evolutionary history. E.g., when exposed to environment 'A', phenotype 'a' is observed, $B \rightarrow b$, $C \rightarrow c$, etc...

By comparing species to one another in this way we can understand general patterns in adaptedness.



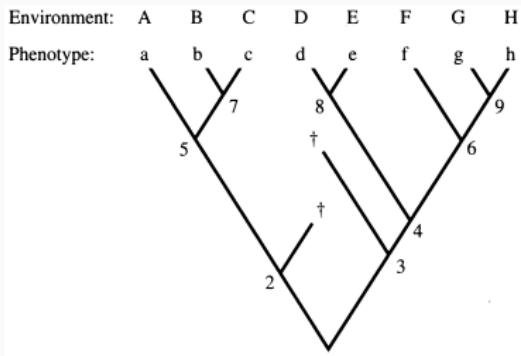
Comparative Methods



Assuming species are adapted to their current environments, extant species can tell us something about their evolutionary history. E.g., when exposed to environment 'A', phenotype 'a' is observed, $B \rightarrow b$, $C \rightarrow c$, etc...

By comparing species to one another in this way we can understand general patterns in adaptedness.

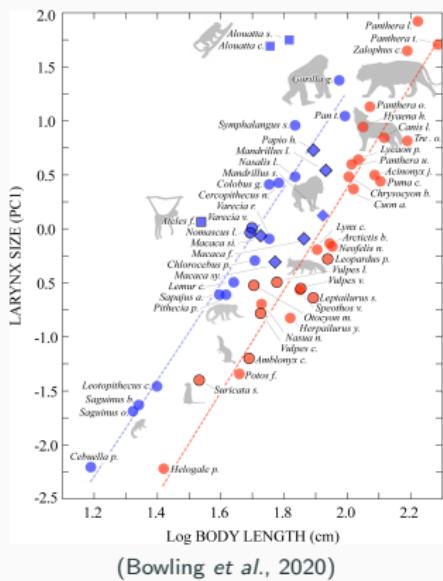
Studying evolution by comparing species is called the **comparative method**.



Comparative Methods cont.



Let's say you're interested in studying the evolutionary relationship between body size and larynx size in mammals.



We can study this by regressing larynx size against body length.

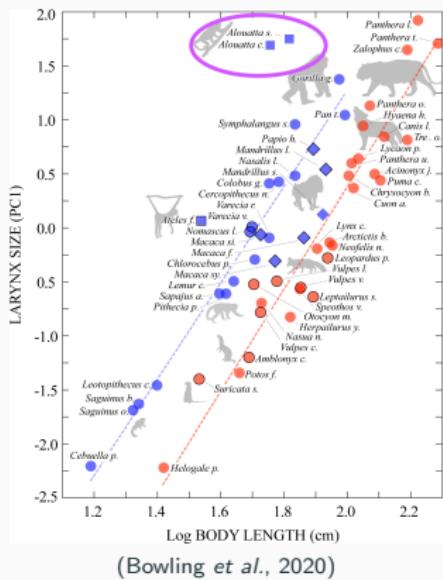
The regression line provides information on the co-evolution of larynx size and body length.

Significant departures from the trend tell us about species that might be worth a deeper dive.

Comparative Methods cont.



Let's say you're interested in studying the evolutionary relationship between body size and larynx size in mammals.



We can study this by regressing larynx size against body length.

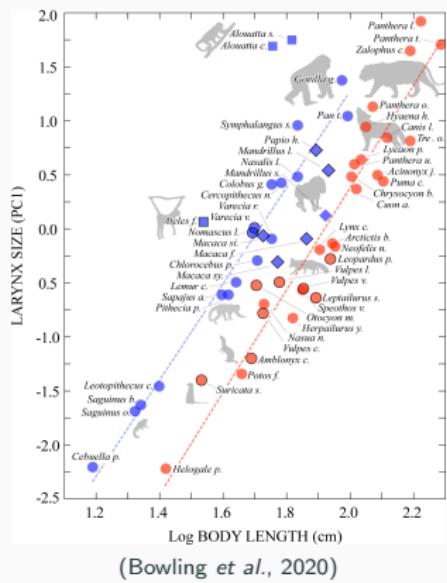
The regression line provides information on the co-evolution of larynx size and body length.

Significant departures from the trend tell us about species that might be worth a deeper dive.

Comparative Methods cont.



Comparative methods have a major pitfall that can impact the reliability of any findings.



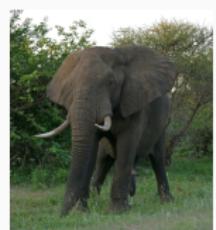
Gorilla gorilla, source: Wikipedia



Elephas maximus sumatrensis, source: Wikimedia



Elephas maximus indicus, source: Pixabay



Loxodonta africana, source: Wikipedia

We probably have new information.

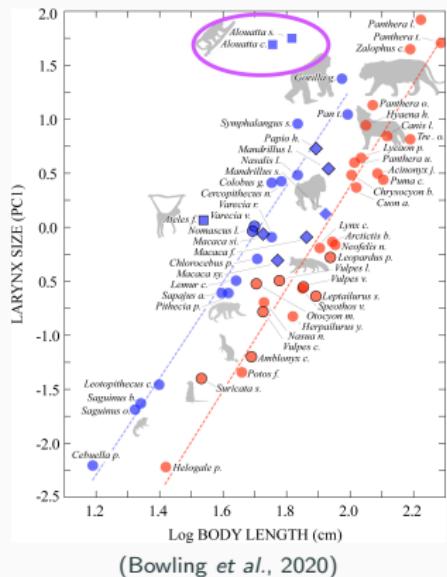
What about now?

Comparative Methods cont.



THE UNIVERSITY OF BRITISH COLUMBIA
Okanagan Campus

Clusters of data from closely related species can have disproportionate effects and pull regressions lines in their direction if not accounted for.



Gorilla gorilla, source: Wikipedia



Elephas maximus sumatrensis, source: Wikimedia

Do we really have completely new information?



Elephas maximus indicus, source: Pixabay

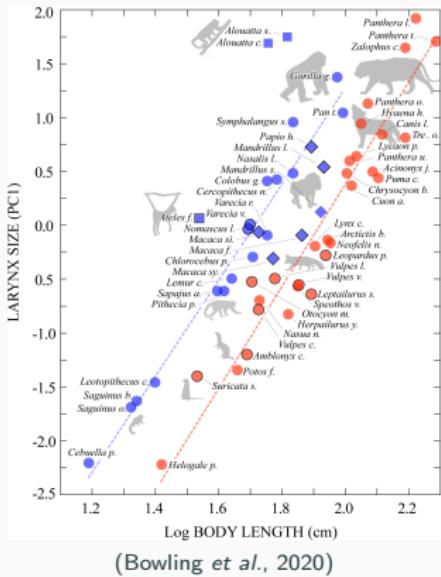


Loxodonta africana, source: Wikipedia

We probably have new information.

What about now? 18

Comparative Methods cont.



This effect comes from something termed 'phylogenetic autocorrelation'.

If not accounted for, phylogenetic autocorrelation can substantially bias comparative methods.

The question then is how do we account for this?

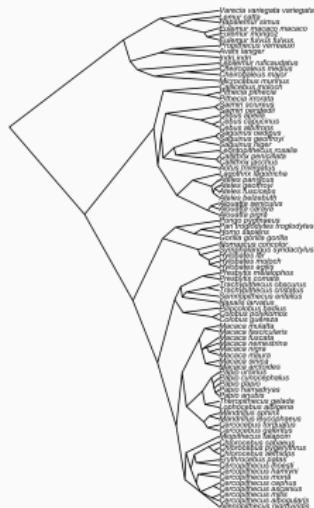
Phylogenetic Inertia

Phylogenetic Inertia



THE UNIVERSITY OF BRITISH COLUMBIA
Okanagan Campus

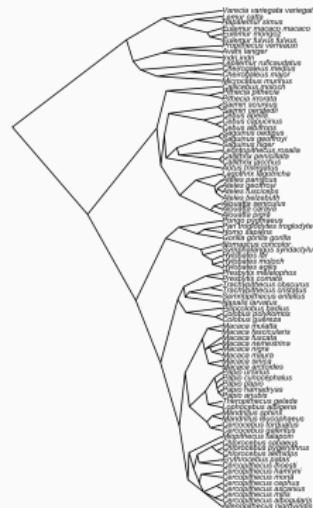
Darwin (1859) recognised that species do not start over from scratch after speciation and that characteristics are built on existing ones that were inherited from their ancestors.



Phylogenetic Inertia

Darwin (1859) recognised that species do not start over from scratch after speciation and that characteristics are built on existing ones that were inherited from their ancestors.

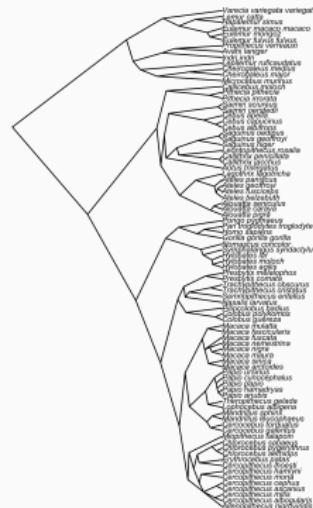
Inheritance will limit the amount of evolution seen in the new taxa,



Phylogenetic Inertia

Darwin (1859) recognised that species do not start over from scratch after speciation and that characteristics are built on existing ones that were inherited from their ancestors.

Inheritance will limit the amount of evolution seen in the new taxa, especially if only a short amount of time has passed (evolutionarily speaking).

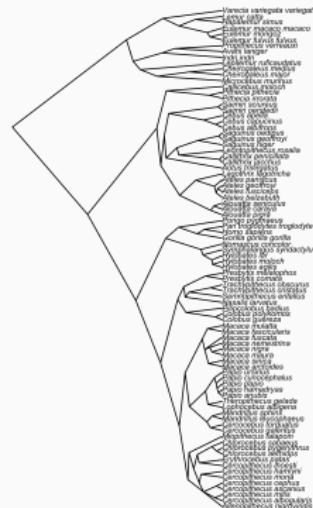


Phylogenetic Inertia

Darwin (1859) recognised that species do not start over from scratch after speciation and that characteristics are built on existing ones that were inherited from their ancestors.

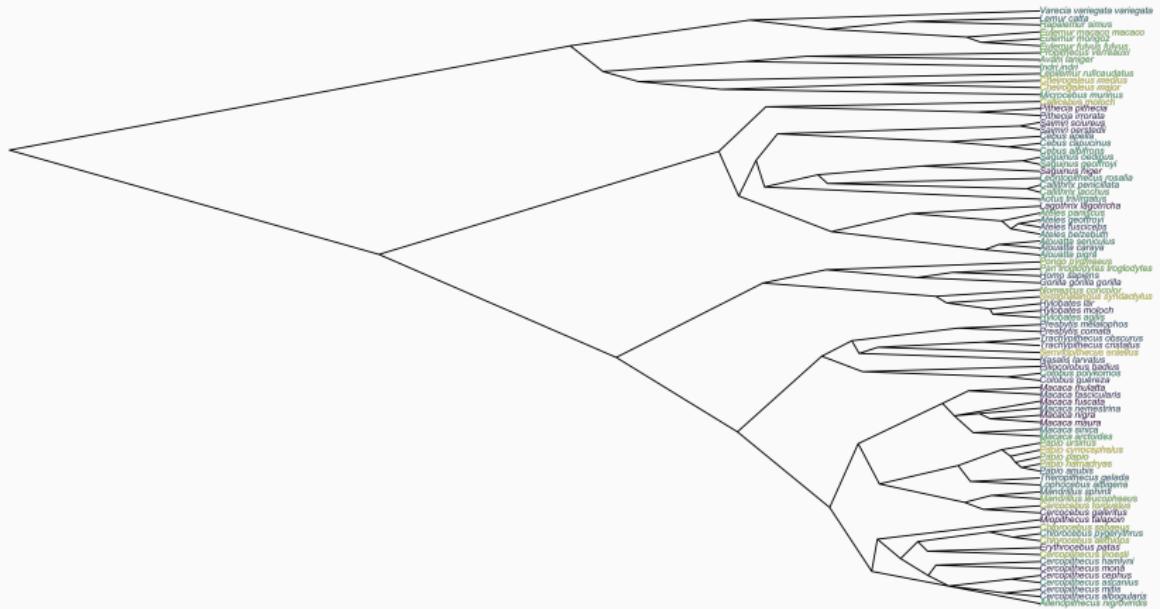
Inheritance will limit the amount of evolution seen in the new taxa, especially if only a short amount of time has passed (evolutionarily speaking).

This phenomenon is referred to as **Phylogenetic inertia**.



Phylogenetic Inertia cont.

Example: In primates, closely related species have similar brain sizes (colours cluster on the tree).



Phylogenetic tree derived from Arnold *et al.* (2010).

Problem:

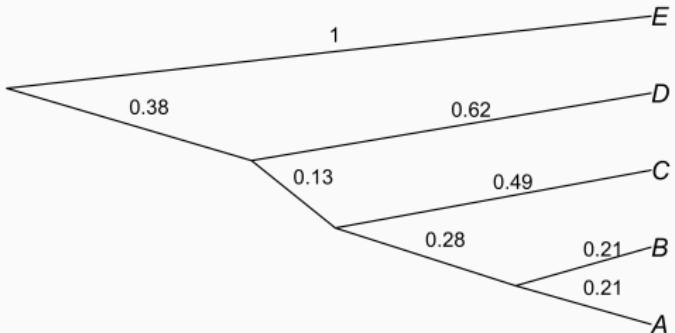
“... species are part of a hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution” — Felsenstein (1985)

Solution:

“The non-independence can be circumvented in principle if adequate information on the phylogeny is available.” — Felsenstein (1985)

In other words, if we can get information on how species are related, we can leverage this information to improve our models.

Phylogenetic Correlation Matrix



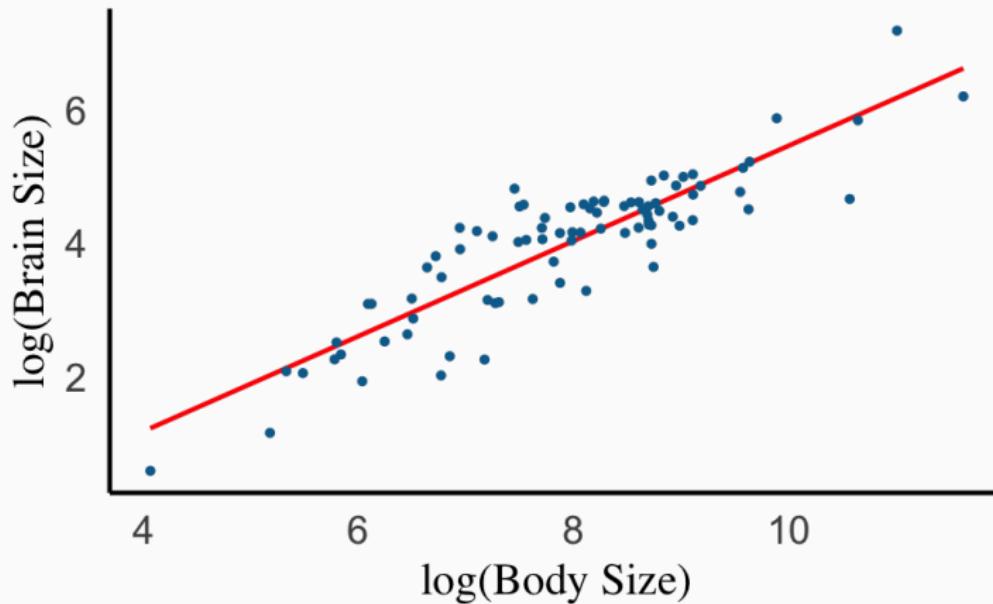
	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>	<i>E</i>
<i>A</i>	1	0.79	0.51	0.38	0
<i>B</i>	0.79	1	0.51	0.38	0
<i>C</i>	0.51	0.51	1	0.38	0
<i>D</i>	0.38	0.38	0.38	1	0
<i>E</i>	0	0	0	0	1

When carrying out comparative analyses we use information on species' relatedness to build a phylogenetic correlation matrix.

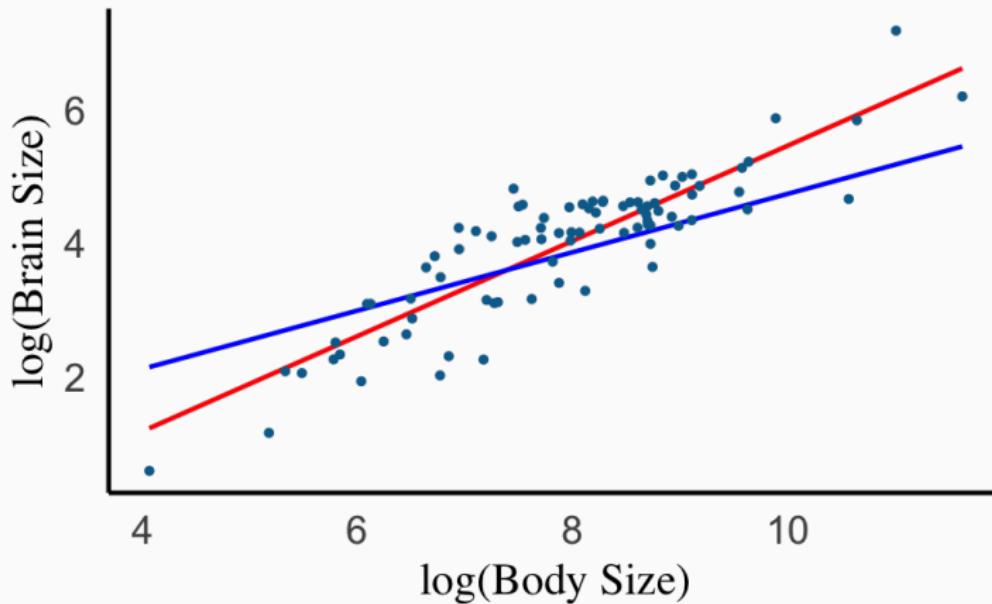


With a phylogenetic correlation matrix in hand, all that's left to do is fit a model that leverages this information.

For example, if we're interested in the evolutionary relationship between primate brain size and body size a simple linear regression model would look like this:



And a model that accounts for the evolutionary relatedness between species (termed a phylogenetic regression model) would look like this:



Limitations of comparative methods

Comparative methods can identify correlations between traits and ecological conditions, but they don't tell us anything about the mechanisms.

They rely on comparing traits across species so there is an upper limit on sample sizes.

They assume that species are adapted to current conditions. Is this a safe assumption?

Comparative methods are a powerful tool for understanding general evolutionary patterns, especially for systems/questions that challenge inference by experimentation.

They are also one of the best tools we have for identifying interesting model species or experimental designs.

Application of the comparative method requires special analytical workflows designed to overcome species' relatedness.

References

- Arnold, C., Matthews, L.J. & Nunn, C.L. (2010). The 10ktrees website: a new online resource for primate phylogeny. *Evolutionary Anthropology: Issues, News, and Reviews*, 19, 114–118.
- Bowling, D.L., Dunn, J.C., Smaers, J.B., Garcia, M., Sato, A., Hantke, G., Handschuh, S., Dengg, S., Kerney, M., Kitchener, A.C. et al. (2020). Rapid evolution of the primate larynx? *PLoS biology*, 18, e3000764.
- Darwin, C. (1859). *On the origin of species by means of natural selection, or the Preservation of Favoured Races in the Struggle for Life*. 1st edn. John Murray, London.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125, 1–15.